MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

VOLUME 14, NUMBER 1 JANUARY, 1957

Contents

PUBLISHED QUARTERLY BY THE CALIFORNIA BOTANICAL SOCIETY

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Entered as second-class matter at the post office at Berkeley, California, January 29, 1954, under the Act of Congress of March 3, 1879. Established 1916. Subscription price $4.00 per year. Published quarterly and issued from the office of Madroño, Herbarium, Life Sciences Building, University of California, Berkeley 4, California.

FORECAST OF A SYSTEM OF THE DICOTYLEDONS

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A standing problem of taxonomic biology — its importance and difficulty made known by the incompletely successful efforts of fully two centuries — is that of the natural and convenient organization of the families of dicotyledons in groups of the category of orders. De Candolle (1813; to him, what we call a family was an order, and what we call an order was a subclass, legion or cohort) remarked of this problem, "C'est là le problème le plus important à résoudre qui se présent aujourd'hui dans l'étude des rapports naturels." And Schnarf (1933) had still to say, "Dagegen ist die Gruppierung der Familien zu Ordnungen oder Reihen schon mit einer gewissen Unsicherheit behaftet, die darin zum Ausdruck kommt, dass die Abgrenzung der Ordnungen von verschiedenen Forschern vielfach in verschiedener Weise vorgenommen wird."

In his work just cited, De Candolle observed that there had been almost as many systems as systematists; which is not far from saying that every systematist has a right to his own system. Among the very many systems which systematists have produced, few have had much influence. During the nineteenth century, the system of De Candolle (of which that of Bentham and Hooker is a variant) overshadowed all others; subsequently, the system of Engler and Prantl has had the same effect. All this is as it should be. We need at every time to have an accepted system, by which we may know where to look for what concerns us in herbaria and manuals. The systems which have been offered as challenges to the accepted systems have brought about minor improvements in the latter. They have had the more important effect of keeping us aware that the accepted system is never the final truth. As the system of Engler and Prantl displaced that of De Candolle, so surely it will be displaced by one which is recognizably a more satisfactory representation of the system which exists in nature.

Considering these things, I took a summons to appear in a symposium as occasion to try to predict the system of the future; this to the extent of formulating the skeleton of a system which is set forth below.

This system gives much weight to microscopic characters, though I can scarcely claim mastery of the great mass of available data. Metcalf and Chalk (1950) give a bibliography of about twenty-five hundred titles, nearly all of them subsequent to the translation of Solereder by Boodle and Fritsch (1908). Schnarf (1931) listed about seventeen hundred contributions to embryology. Wodehouse (1935) listed some three hundred

[1] It was a high honor, accepted with diffidence, to be asked to speak on "Anatomy and taxonomy" in a symposium commemorating the fiftieth anniversary of the Botanical Society of America, on August 28, 1956, at the meeting of the American Institute of Biological Sciences at the University of Connecticut. The present paper is a revision of the one given on that occasion.

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papers on pollen grains, and Erdtmann (1952) about eleven hundred in the same field. Where study of vascular anatomy, at Harvard and elsewhere, has yielded definite conclusions, it has been possible to formulate orders with considerable confidence; for the rest, the orders are those of Engler and Prantl with certain amendments suggested by embryological or palynological data.

Large orders are preferred to small: in maintaining an order of two or three families, one is not far from leaving the families unplaced. However, it has not been found possible to be consistent in this matter. It is not considered necessary that the orders be definable by description.

Names are applied to the orders according to the principles of priority and typification. The experience of very many taxonomists has shown it necessary to apply these principles in dealing with genera and species. Experience with the formulation and naming of higher groups has been comparatively scant. Perhaps for this reason, taxonomists in convention have taken the position that it is possible to make defensible choices among the fairly numerous names which have been applied to higher groups without recourse to the principles cited. Whether or not this position is sound, no novelties are here added to the synonymy of ordinal names.

Subclass DICOTYLEDONES Lindley

Synops. British Fl. 4 (1829).

Order 1. Multisiliquae L. Gen. Pl. ed. 6 (1764). Orders *Piperitae* and *Coadunatae* L. op. cit. Orders *Piperinae* (Brongniart, as class) and *Polycarpicae* (Endlicher, as class) Braun in Ascherson Fl. Brandenburg 1: 36, 47 (1864). Orders *Piperales* and *Ranales* Engler Syllab. 93, 106 (1892).

Among names of the three natural orders in which Linnæus placed these plants, that of which the apparent typical genus is *Ranunculus* is preferred to those of which the apparent typical genera are respectively *Piper* and *Magnolia*.

This order includes the generality of dicots with apocarpous flowers, as well as some of their immediate derivatives. They have been studied extensively by Bailey and his associates (Bailey and Nast, 1943, 1944, 1945; Bailey, Nast, and Smith, 1943; Bailey and Smith, 1942; Bailey and Swamy, 1949; Smith, 1943, 1945, 1946, 1947; Swamy, 1949; Swamy and Bailey, 1949). These scientists are authority for the assemblage here of a large number of families, including the Piperaceæ and their immediate allies. To current botanical opinion, this is definitely the primitive order of flowering plants. Some families are homoxylous, *i. e.*, having wood without vessels, in contrast to the heteroxylous condition which is characteristic of flowering plants. In some families the pollen grains are monocolpate, *i. e.*, marked by a single groove; this character they share with the generality both of the lower seed plants and of the monocots, while in typical dicots the pollen grains are tricolpate or of more elaborate types derived from this. The two primitive characters mentioned, and the peculiar

anatomical character of oil cells in the tissues, are distributed among the families of Multisiliquæ each one in seeming independence of the others. This means that, quite as one would expect of a primitive group, the families are isolated or fall into isolated blocks. It is necessary as a matter of convenience to maintain the order as a whole; it is not possible to divide it into a small number of natural orders. The families are as follows:

a. Homoxylous, pollen monocolpate: Winteraceæ.

b. Heteroxylous, pollen monocolpate: Degeneriaceæ, Himantandraceæ, Magnoliaceæ, Anonaceæ, Eupomatiaceæ, Myristicaceæ, Canellaceæ, Monimiaceæ, Gomortegaceæ, Lauraceæ, Hernandiaceæ, Lactoridaceæ, Calycanthaceæ, Chloranthaceæ, Piperaceæ, Saururaceæ.

c. Wood degenerate, pollen monocolpate: Nymphæaceæ (pollen tricolpate in subfamily Nelumbonoideæ).

d. Homoxylous, pollen tricolpate: Trochodendraceæ, Tetracentraceæ.

e. Heteroxylous, pollen tricolpate: Eupteleaceæ, Cercidiphyllaceæ, Illiciaceæ, Schisandraceæ, Berberidaceæ, Menispermaceæ, Lardizabalaceæ, Ranunculaceæ.

Order 2. Juliflorae (Endlicher as class) Braun in Ascherson Fl. Brandenburg 1: 62 (1864). Order *Amentaceæ* of Linnæus and Jussieu: one would not maintain a name in *-aceæ* as that of an order. Tippo (1938), on the basis of studies of the anatomy of the wood, assembled the families Hamamelidaceæ, Platanaceæ, Myrothamnaceæ, Stachyuraceæ, Betulaceæ, Fagaceæ, and Casuarinaceæ, as a natural group derived immediately from Multisiliquæ.

It is an annoyance to have no definite opinion as to the natural place in the system of the familiar families Salicaceæ and Juglandaceæ. Gundersen (1950) grouped Juglandaceæ with Myricaceæ and Rhoipteleaceæ, which may well be sound; but there is not much to tell where the group belongs.

Order 3. Scabridae L. Order *Urticæ* Jussieu, the mere plural of a generic name. Order *Urticinæ* (Bartling as class) Braun. Order *Urticales* Engler Syllab. 95 (1892). Ulmaceæ, Eucommiaceæ, Moraceæ, Urticaceæ. Study of the woods by Tippo (op. cit.) was held to confirm this generally-accepted group as natural, and to show that its origin was from the lower Julifloræ.

Order 4. Guttiferae Jussieu Gen. Pl. 225 (1789). Suborder *Theineæ,* Theaceæ, Marcgraviaceæ, Caryocaraceæ, Medusagynaceæ, Clusiaceæ, Hypericaceæ, Quiinaceæ, Eucryphiaceæ, Ochnaceæ, Dipterocarpaceæ. Vestal (1937) found the anatomy of the woods to confirm as natural this generally accepted assemblage of families. They show nice transitions from primitive vessels with barred perforations to advanced vessels with porous perforations. Similarly in the flowers, there are transitions from spiral parts of indefinite numbers to whorled parts of definite numbers, while the endosperm varies from nuclear to cellular (Schnarf on *Saurauia,* 1924; Swamy on *Marcgravia,* 1948). The basic family Dilleniaceæ is

needed to bind together this assemblage; it might otherwise as well be included in Multisiliquæ.

Order 5. BICORNES L. Orders *Rhododendra* and *Ericæ* Jussieu Gen. Pl. 158, 159 (1789). Order *Ericales* Engler Syllab. 151 (1892). The vessel perforations vary in the Bicornes from barred to porous. The flowers are characteristically sympetalous (there are both primitive and derived examples with separate petals); the stamens are free of the corolla, with no ribbed endothecium (except in the primitive family Clethraceæ), the anthers opening through pores, the pollen grains united in tetrads. The endosperm is cellular: the first two divisions of the endosperm mother cell are transverse, producing a row of four cells, among which the terminal members give rise to haustoria. Nearly all authorities agree that this group is immediately related to *Saurauia,* which belongs in or next to Actinidiaceæ. The families are Clethraceæ, Ericaceæ, Empetraceæ, and Epacridaceæ. In many Epacridaceæ, the stamens are epipetalous and the anthers open through slits, and the pollen grains are solitary; but these plants are linked to Ericaceæ by clear lines of transition. The families Lennoaceæ and Diapensiaceæ, which have been placed in this order, do not belong to it, and are for the present left unplaced.

Order 6. GUIACANAE Jussieu Gen. Pl. 155 (1789). Order *Diospyrinæ* (Brongniart as class) Braun in Ascherson Fl. Brandenburg 1: 37 (1864). Order *Ebenales* Engler Syllab. 155 (1892). Styracaceæ, Sapotaceæ, Symplocaceæ, Ebenaceæ, and other families. De Candolle condemned *tatonnement* (fumbling!) as a method of recognizing the natural system; yet it was the accident that I have *Styrax* in near-by foothills and a plant of *Camellia* in my back yard that enabled me to see that Styracaceæ is immediately related to Theaceæ.

Order 7. PASSIFLORINAE (Brongniart as class) Braun in Acherson Fl. Brandenburg 1: 50 (1864). Order *Rotaceæ* L., in part. Order *Cisti* Jussieu, the mere plural of a generic name. Order *Parietales* (Endlicher) Braun op. cit. 49. *Cistifloræ* Eichler. Vestal (1937) assembled the families Flacourtiaceæ, Bixaceæ, Cochlospermaceæ, and Cistaceæ as a natural group descended directly from Multisiliquæ. Whether the herbaceous families Passifloraceæ, Caricaceæ, Cucurbitaceæ, and Begoniaceæ, usually placed with these, belong with them or belong together, and whether Violaceæ and Resedaceæ belong with them, is apparently as yet uncertain.

Order 8. SENTICOSAE L. op. cit., the evident standard genus being *Rosa.* Orders *Papilionaceæ, Lomentaceæ,* and *Pomaceæ* L. Order *Rosifloræ* (Endlicher) Braun. Order *Rosales* Engler Syllab. 115 (1892). Tippo (1938) showed that Saxifragaceæ *sens. lat.*, Brunelliaceæ, Cunoniaceæ, and Rosaceæ belong together. Presumably Crassulaceæ, Pittosporaceæ, and Leguminosæ belong with them. They are derived directly from woody Multisiliquæ.

Order 9. RHOEADEAE L., including orders *Corydales, Putamineæ,* and *Siliquosæ* L. Order *Rhoeadinæ* (Bartling as class) Braun. Order *Rhoeadales* Engler Syllab. 111 (1892). Papaveraceæ, Tovariaceæ, Fumariaceæ, Capparidaceæ, Cruciferæ; Moringaceæ and Violaceæ have been placed here. They are believed to be derived directly from Multisiliquæ.

To this point in this presentation, it is believed that the truth as to the main outline of the phylogeny of the dicots has been perceived. The order Multisiliquæ is primitive; Julifloræ, Guttiferæ, Passiflorinæ, Senticosæ, and Rhoeadeæ are immediate derivatives; Scabridæ, Bicornes, and Guiacanæ are secondary derivatives. A considerable number of further orders are recognizable, but their connections are less clear. Gundersen (1950) took note that most compound pistils with axile placentation pass during development through a stage in which the placentation is parietal. Considering this fact in connection with the principle that ontogeny recapitulates phylogeny, he thought it probable that the group here called Passiflorinæ is an important secondary center of variation, ancestral to most of the remaining dicots. It is arguable, on the contrary, that parietal placentation is not usually a primitive character, but a result of pædogenesis, that is, of courses of evolution by which the immature condition of a relatively primitive organism becomes the mature condition of its derivatives. Hallier (1905) would have derived many of the more advanced dicots from Sterculiaceæ. Purely as a speculation, it is here suggested that more orders than Bicornes and Guiacanæ may be derived from Guttiferæ.

Order 10. PRECIAE L., including orders *Rotaceæ, Caryophyllei,* and *Holoraceæ* and *Succulentæ* L. in part. Orders *Curvembryæ, Centrospermæ, Polygonales, Opuntales, Primulales,* and *Plumbaginales* of Engler and others. A matter of fifteen families, decidedly varied in gross characters. The bulk of the families are characterized by curved or coiled embryos. Schnarf (1931, 1933) found Opuntiaceæ definitely linked to these, perhaps in the neighborhood of Aizoaceæ, by embryological characters. The embryos are straight or nearly so in Polygonaceæ (in which the anatomy of the stem is anomalous, as it is also in Amaranthaceæ and Chenopodiaceæ), Primulaceæ (notably similar to Caryophyllaceæ in gross features) and Plumbaginaceæ (distinguished by embryological peculiarities).

In the middle of the Englerian system of the dicots, there is a long series of families, from Pandaceæ to Cynomoriaceæ, of which the majority are mere names to European and North American field botanists. Engler assembled many of these as two orders distinguished by the position of the ovules. In Geraniales, the ovule is epitropous, "turned up," either erect with the micropyle turned in or pendant with the micropyle turned out. In Sapindales, the ovule is apotropous, "turned down," either erect with the micropyle turned out or pendant with the micropyle turned in. The extensive study of woods principally of these families by Heimsch (1942) appears to have revealed a more natural grouping than the Englerian: the next three orders represent it.

Order 11. Polygalinae (Brongniart as class) Braun in Ascherson Fl. Brandenburg 1: 36 (1864). Order *Polygalales* (Bessey as suborder, 1897) Hallier (1905). Wood with rays hetrogeneous I or II A; parenchyma in apotracheal bands or scantily paratracheal; fiber-tracheids with conspicuously bordered pit-pairs. Humiriaceæ, Linaceæ, Erythroxylaceæ, Polygalaceæ, Krameriaceæ, Diclidantheraceæ, Trigoniaceæ, Tremandraceæ, Zygophyllaceæ, Malpighiaceæ, Vochysiaceæ.

Order 12. Trihilatae L. Order *Terebinthinæ* (Bartling) Braun. Order *Terebinthales* Wettstein. *Pinnatæ* Hutchinson. Rays heterogeneous II B or homogeneous; parenchyma banded or paratracheal; wood fibers with simple pits. Rutaceæ, Cneoraceæ, Simarubaceæ, Meliaceæ, Sapindaceæ, Hippocastanaceæ, Aceraceæ, Bretschneideraceæ, Connaraceæ, Burseraceæ, Terebinthaceæ. Julianiaceæ is to be reduced to Terebinthaceæ.

The action of botanical congresses in conserving numerous names of families was scarcely duly considered, since practically all of these names are valid by the letter of the code. As an exception, the name Terebint(h)aceæ (Jussieu as order) appears to have been applied definitely to a family before Anacardiaceæ was.

Order 13. Gruinales L. Order *Geraniales* Engler. The wood (of woody examples) exhibits advanced characters, absence of scalariform perforations and presence of libriform fibers. Geraniaceæ, Oxalidaceæ, Tropæolaceæ, Balsaminaceæ. Limnanthaceæ, a small family of herbs of western North America, are in gross structure closely similar to Geraniaceæ. They are embryologically peculiar (having a 4- or 2-sporic embryo sac of unique type; Mason, 1951; Mathur, 1956), but may as well be placed here.

Order 14. Tricoccae L. Euphorbiaceæ, an enormous family, chiefly tropical, grossly varied in every character as though not a natural group.

Order 15. Columniferae L. Order *Malvales* Engler. Tiliaceæ, Malvaceæ, Bombacaceæ, Sterculiaceæ, and other families; a thoroughly natural group.

Order 16. Calycanthemae L. Orders *Calycifloræ* and *Hesperideæ* L., in part. Order *Myrifloræ* (Endlicher) Braun. Loasaceæ, Thymelæaceæ, Elæagnaceæ, Lythraceæ, Onagraceæ, Melastomaceæ, Myrtaceæ, and many others; needing further study.

Order 17. Umbellatae L. Order *Hederaceæ* L., in part. Order *Umbellifloræ* (Bartling as class) Braun. Cornaceæ, Araliaceæ, Umbelliferæ. The suggestion that Garryaceæ also belongs here has been confirmed by a recent thorough study by Moseley and Beeks (1956).

Order 18. Santalinae Grisebach. Like Calycanthemae and Umbellatæ, these have choripetalous flowers with inferior ovaries; the characters may be obscured by reduction. Olacaceæ, Santalaceæ, Loranthaceæ, Balanophoraceæ, etc.

Among sympetalous dicots, the Bicornes, Guiacanæ, and Primulales

have already been given places. As to the remainder, the evidence, particularly from the embryology, inclines one to treat them as a natural group of four orders, as follows.

Order 19. LURIDAE L., including orders *Campanaceæ* L. (Convolvulaceæ and Polemoniaceæ), *Personatæ* L. (Scrophulariaceæ, etc.), *Asperifoliæ* L. (Hydrophyllaceæ and Boraginaceæ) and *Verticillatæ* L. (Labiatæ). Order *Tubifloræ* (Bartling as class) Braun. About twenty-three families. In Bicornes and Guiacanæ, the cellular endosperm is inherited from certain Guttiferæ. In the present order it has evolved separately, the lower families, Convolvulaceæ and Polemoniaceæ, having nuclear endosperms. Whereas in Bicornes the endosperm mother cell undergoes two transverse divisions and produces a linear four-celled endosperm, in the present order it undergoes usually a transverse division followed by a longitudinal division, producing a T-shaped stage. The apetalous family Callitrichaceæ has the embryogeny of this group.

Order 20. CONTORTAE L., including *Sepiariæ* L. Seven families, a very natural group, apparently a minor offshoot of the preceding.

Order 21. STELLATAE L. Caprifoliaceæ and Rubiaceæ. The Adoxaceæ have the pollen of this group (Erdtmann, 1954).

Order 22. AGGREGATAE L. Eight families, including Campanulaceæ, Lobeliaceæ, Valerianaceæ, Dipsacaceæ, and Compositæ. In the Englerian system, part of these are in Rubiales, but the embryological characters (and, indeed, the characters in general) place them as here.

A large number of families remain unplaced. Places could be given to many of them by recognizing such orders as Juglandales, Aristolochiales, Sarraceniales, and Celastrales; but these are either small and themselves not certainly placed, or else not evidently natural. Surely, by sufficient study of anatomy, embryology, and palynology, we will eventually learn their true positions.

At the same meetings and on the same day on which this paper was given oral presentation, Dr. Arthur Cronquist presented a system of the dicots which is expected soon to reach publication. Cronquist places all of the families in orders, which, for the sake of definition by description, are made considerably smaller and more numerous than the ones here maintained. The orders are arranged in a phylogenetic pattern with which the one here presented is in essential agreement so far as it goes. The differences between his system and mine are as though we were artists representing the same tree under the conventions of different schools, and as though he had seen many more details than I (I have every reason to believe that he has perceived most of them correctly). The points of agreement allow us to believe that we are actually approaching the system of the future.

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A BOTANICAL DISASTER

ERWIN F. LANGE

A chance meeting of two botanical explorers along the shores of the Columbia near The Dalles, Oregon, on November 13, 1843, left a story of disaster which completely altered the life of a German botanist, Frederick George Jacob Lueders. For on that day Lueders stood by helplessly as he watched the turbulent Columbia swallow up his entire botanical collection and collecting equipment. In a matter of seconds the results of three years' labor in the wild and mountainous parts of the United States were washed away. All that Lueders was able to rescue from the water was a treasured copy of his Torreý and Gray Flora.[1] This event would probably have gone unrecorded in the pages of Northwest science history had it not been for the famed United States explorer, Captain John C. Fremont, who witnessed the event and noted it in his journal. Concerning the calamity he wrote:

> A gentleman named Lueders, a botanist from the city of Hamburg, arrived at the bay I have called by his name, while we were bringing up the boats. I was delighted to meet at such a place a man of kindred pursuits; but we had only the pleasure of a brief conversation, as his canoe, under the guidance of two Indians, was about to run the rapids; and I could not enjoy the satisfaction of regaling him with breakfast, which after his recent journey, would have been an extraordinary luxury.
>
> All his few instruments and baggage were in the canoe, and he hurried around to meet it at Grave Yard Bay; but he was scarcely out of sight when, by the carelessness of the Indians, the boat was drawn into the midst of the rapids, and glanced down the river, bottom up, with a loss of everything it contained. In the natural concern I felt for his misfortune, I gave to the little cove the name of Lueders' Bay.

Fremont's note aroused but little interest until Leslie L. Haskins came to Brownsville, Oregon, as a photographer and botanist. As a small boy in

[1] This book is today a part of the library collection of the Oregon Historical Society. Augusta Lueders, a daughter of the German botanist, sent it to Leslie L. Haskins, author of "Wild Flowers of the Pacific Coast," who presented it to the Historical Society library.

Sauk City, Wisconsin, around 1890 he had often seen and heard of an old German gardener and botanist, Frederick G. J. Lueders, a resident of that community. On coming to Oregon, Haskins was surprised to find that no one could give him information regarding the life and activities of the German botanical explorer. Only as the result of an intensive correspondence was Haskins able to uncover the story of Lueders' life. The material was supplied by Miss Augusta Lueders, daughter of the botanist.

Frederick Lueders was born in Hamburg, Germany, on October 3, 1813, the son of a gardener. In Hamburg he attended a private school and later studied botany at the Hamburg Botanical Gardens. Then he entered the large seed house of Haage in Erfurth, Saxony. On returning to Hamburg, the Society for Natural Science offered Lueders the opportunity for scientific exploration in the United States. To qualify for the opportunity, Lueders again attended school to learn navigation, and at graduation he qualified for first mate.

Concerning the coming years of his life, Lueders wrote[2] a friend in 1861:

> I arrived in Sauk Prairie in July, 1841, in company with my friend . . . We reached Green Bay by way of the lakes, and passed through the richly wooded country, which borders upon the Fox River and Lake Winnebago. Leaving the forest and entering the open country, we were much surprised at the beauty of the natural park. At that early time a few farms only guided the stage road. In almost every house where we stopped, the hospitable people invited us to spend a few days at their new home, and share what their humble plantation could afford, of course without pay. Arrived at Fort Winnebago, the terminous of the stage. The fortification was still garrisoned; there was besides a store, tavern and blacksmith's shop near the fortress. From there we went down the Wisconsin River by a boat of the French fur trader.
>
> I spent the rest of the season about Sauk prairie in collecting several hundred species, in part, very interesting plants.
>
> Although I did not intend to spend the winter there, I was surprised by it before I could find conveyance to the Mississippi.
>
> In March, 1842, I went to Galena, And from there to St. Louis. There I found an easy introduction in my pursuit, as a Dr. Asa Gray, of New York, had kindly furnished me with a letter to Dr. Engelmann, whose services for the development of Western horticulture are amply known.
>
> After a short stay in the city I proceeded to search the western part of Missouri, collecting plants and curiosities. On my excursion to that part of Missouri, I found opportunity to gather information about the Western country, and resolved to pursue the next spring a westerly course as far as terra firma would permit me to study and collect the flora of the mountainous country. In the meantime there had awakened a spirit of emigration to Oregon, and large bodies of emigrants were along the frontier of Missouri forming several companies. One of these I joined leaving the civilized world in May, 1843.
>
> In the course of the journey, I collected plants and noted down peculiarities as circumstances would permit.
>
> The loss of my baggage in the rapids below the Grand Cascades of the Columbia River, rests not only severe with the collection of plants, but perhaps more so with a good many valuable instruments and other collecting material, as I had fitted myself out to spend several years in that part of the country.

---

[2] Letter in herbarium, University of Oregon, Eugene.

The kindest assistance was offered me by the gentlemanly officers of Fort Vancouver, but could not lead me into the course which my enthusiastic mind had marked out, and from there all communication by letter was tedious and uncertain. I concluded to return to Europe and engage anew, after having gained some useful experience.

In February, 1844, I left the mouth of the Columbia River for the Sandwich Islands, and proceeded from there to Chile, touching the Paradise of the Pacific (Otaheite), then in a state of siege. I arrived in Hamburg in November of the same year.

In the short space of my absence, family circumstances had taken a change, that made my presence there, at least for several years, necessary. So the course nearest my heart, for future life, was beyond my individual control.

At Christmas, 1844, I again hailed the Mississippi. I lived at St. Louis until 1851, and after that time in Sauk County (Wisconsin) tilling the soil and my mind.

— F. G. J. Lueders

He spent the rest of his life in Sauk City, Wisconsin, and engaged in many astronomical studies. In 1869 he had published in Hamburg "The Aurora Borealis and Law of Reciprocal Action in the Universe" and in 1884 the University of Wisconsin published his observations on a number of Auroras which he had studied. Privately, Lueders also published a pamphlet "Memoirs on Physical Astronomy." For many years he was city treasurer of Sauk City. He died December 21, 1904.

Thus a botanical disaster prevented Lueders' name from being associated with Northwest botany. Had his specimens been properly reported, there is no doubt that his name would have been linked with species of western plants. Lueders' Bay, named by Fremont, is also a lost geographical name. One can only speculate on its location, and as the large dams on the Columbia are changing the topography along the river, Lueders' Bay itself may no longer be in existence.

Portland State College,
Portland, Oregon

ROBERT HIBBS PEEBLES[1]

The death, last March, of Robert Hibbs Peebles, one of the world's leading cotton breeders and an outstanding student of cotton genetics, was a great loss to southwestern agriculture. He was the originator of what had become, in recent years, the preferred variety of Pima (American-Egyptian) long-staple cotton, and carried on investigations of the inheritance of various characters of this very important crop-plant. Toward the end of his career he was working on the problem of how to insure the greatest possible degree of natural cross-pollination, in view of the fact that artificial cross-pollination of cotton varieties usually increases the yield, as compared with that of either parent. The endeavor was to do, with cotton, what has been done so successfully with hybrid corn.

[1] This paper was in press at the time of Dr. Kearney's death on October 19, 1956. —Ed.

FIG. 1. Robert H. Peebles at his home, Sacaton, Arizona, Christmas Eve, 1944.

The University of Arizona, recognizing the great value of Peebles' contributions to the agriculture of the state, conferred upon him an honorary D. Sc., less than a year before his untimely death, at the age of 55. He was also given, posthumously, the United States Department of Agriculture's Superior Service award and medal.

To taxonomic botanists, Dr. Peebles was well-known as an ardent student of the native flora and co-author with me of "Flowering Plants and Ferns of Arizona" (1942) and "Arizona Flora" (1951). For two decades he devoted many of his week-ends to plant collecting in all parts of the state and added substantially to the number of species known to occur there.

He was especially interested in the Cactaceæ, which are such a conspicuous element of the Arizona flora, and he became a recognized authority on that family. The technique which he developed for preparing herbarium specimens of cacti has never been excelled. Some readers of this notice will recall his exhibition of specimens and photographs at a meeting of the California Botanical Society in April, 1953. His name is commemorated in that of the remarkable and very rare little cactus, *Navajoa Peeblesiana* Croizat.

The many friends of Bob Peebles will remember him always for his vivid and lovable personality. He was so very much alive that we can scarcely realize, even yet, that he is no longer with us. He has left a void that will be very hard to fill.—THOMAS H. KEARNEY, California Academy of Sciences, San Francisco.

THE CHROMOSOMAL AND DISTRIBUTIONAL RELATIONSHIPS OF LUPINUS TEXENSIS AND L. SUBCARNOSUS (LEGUMINOSAE)

B. L. TURNER

The genus *Lupinus* is represented in Texas by several species (Shinners, 1953). Of these, the two most commonly encountered are *L. texensis* Hook. and *L. subcarnosus* Hook. The latter taxon is the official state flower of Texas, though *L. texensis* is sometimes mistaken for this species. Both species are endemic to the state and are known locally as bluebonnets. They are probably the most important native rangeland legumes in central Texas, often occupying hundreds of acres of rolling hillsides during the early spring months. The roots of these species are highly nodulated and are undoubtedly important soil nitrifiers. In addition, *L. texensis* has become a popular garden ornamental in many parts of the world. (Although many trade catalogues list *L. subcarnosus* as the Texas bluebonnet, most of the material on the open market appears to be *L. texensis*.)

GEOGRAPHICAL DISTRIBUTION

Lupinus texensis occurs naturally on open calcareous soils throughout central Texas. *Lupinus subcarnosus* is restricted to sandy soils of south-central Texas. The interfingered distribution of the two species (Fig. 1) can be related to alternating grassland — forest strips which occur on deep clay and sandy soils respectively. The ecotone between these vegetative types is sharp, and consequently both species may be found growing in close proximity along many miles of the contact area. *Lupinus texensis* has a wide ecologic amplitude and may grow in a variety of disturbed soil types. As a result, the species has become established along road shoulders which cross the otherwise unoccupied sandy lands, particularly as a result of deliberate sowing by state highway workers and other wildflower enthusiasts. *Lupinus subcarnosus* is rarely if at all sown along highways, and in no instance has the author seen the plant growing naturally on clay soils or along highways in such areas. In the numerous cases where both species were found growing together during the spring of 1955, no sign of morphologic intergradation, meiotic irregularity, or other evidence of hybridization could be detected.

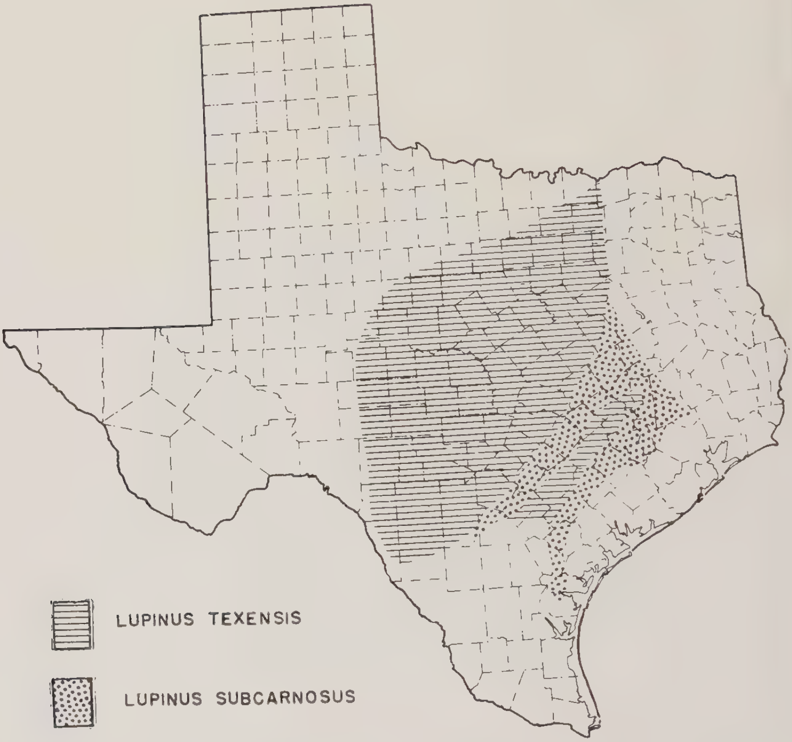


FIG. 1. Probable natural distribution of *Lupinus texensis* and *L. subcarnosus*. Based on herbarium records at The University of Texas and extensive field observation. Further explanation in text.

Chromosome Numbers

Previous to the present study, two different counts had been reported for *L. subcarnosus*. Savchenko (1935) reported 2n = 48 and Tuschnjakowa (1935) reported 2n = 36 for this species. Because of the past confusion in the application of the names *L. texensis* and *L. subcarnosus* (Shinners, 1953), it was at first thought that the two differing counts might be for *both* species instead of *L. subcarnosus* alone. As a result, meiotic studies[1] of natural populations of these two taxa were undertaken. However, it was soon discovered that both *L. texensis* and *L. subcarnosus* had the same chromosome number of n = 18. In all instances, meiosis was completely regular, metaphase plates showing 18 bivalents and anaphase plates were without bridges. Counts obtained are given in Table 1.

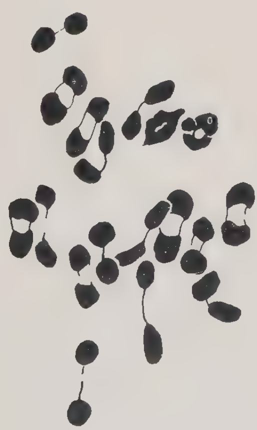
[1] Buds were killed and fixed in a mixture of 4 chloroform:3 absolute alcohol:1 glacial acetic acid. Anthers were squashed in acetocarmine 2 to 3 days after collection. Voucher specimens are deposited at the University of Texas Herbarium, Austin, Texas.

TABLE 1. CHROMOSOME COUNTS OF LUPINUS SUBCARNOSUS AND L. TEXENSIS

Species	Collection	n number
L. subcarnosus	Bastrop County: Bastrop State Park. *Turner 3703.*	18
L. subcarnosus	Bastrop County: 4 miles west of Bastrop. *Turner 3704.*	18
L. subcarnosus	Gonzales County: near Palmetto State Park entrance. *Turner 3708.*	18
L. subcarnosus	Fayette County: 2 miles west of Moulton. *Turner 3712.*	18
L. subcarnosus	Lavaca County: Sublime. *Turner 3719.*	18
L. subcarnosus	Colorado County: 5 miles west of Altair. *Turner 3723.*	18
L. subcarnosus	Fort Bend County: 0.5 mile east of Fulshear. *Turner 3727.*	18
L. subcarnosus	Austin County: San Felipe State Park. *Turner 3730.*	18
L. texensis	Travis County: Austin. *Turner 3699.*	18
L. texensis	Lavaca County: 2 miles west of Moulton. *Turner 3713.*	18
L. texensis	Lavaca County: 1 mile southeast of Shiner. *Turner 3718.*	18
L. texensis	Austin County: 3 miles east of Ulm. *Turner 3732.*	18
L. texensis	Hays County: 10 miles west of San Marcos. *Turner 3733.*	18
L. texensis	Llano County: 3 miles northwest of Buchanan Dam. *Turner and Johnston 2523.*	18

Savchenko's number of 2n = 48 was apparently for some misnamed taxon, or else strains of *L. subcarnosus* and/or *L. texensis* exist in the ornamental trade as derived polyploids. Savchenko did not cite voucher material but merely indicated that the counts were made from seeds obtained from Germany.

2



3

FIGS. 2–3. Metaphase chromosomes of *Lupinus texensis* and *L. subcarnosus: 2, L. texensis,* n = 18; *3, L. subcarnosus,* n = 18. Camera lucida drawings, × 2000.

Discussion

Lupinus texensis and *L. subcarnosus* are apparently very closely related as shown by their external morphological characters and their similar chromosome complements. However, they are clearly separated ecologically and in the field they are reproductively isolated. The reproductive isolation is perhaps partially due to the self-pollinating nature of the breeding populations; naturally occurring cross-pollinated individuals are probably rare. Experimental hybridization between these two species is being undertaken.

The discovery that both *L. texensis* and *L. subcarnosus* have chromosome numbers of n = 18 has certain phyletic implications. Senn (1938), on the basis of Tuschnjakowa's reported number for *L. subcarnosus,* considered the species to be triploid in origin and thus, along with 2n counts of 48 in other species, concluded the base number for the genus to be x = 12 instead of 8, 9, 10, etc., as has been indicated by other workers (Darlington and Janaki-Ammal, 1945). Senn considered species with n numbers of 20, 21, 25, etc. to be derived aneuploids. The only other number of n = 18 reported for the genus *Lupinus* is that made by Eickhorn (1949) on *L. tassilicus* Maire.

Summary

The distributional relationship of *L. texensis* and *L. subcarnosus* has been indicated. The former species is widespread throughout central Texas, occurring in calcareous soils; the latter is more restricted in range, occurring on sandy soils of south-central Texas. Meiotic counts from a number of localities in central Texas showed the chromosome number of both species to be n = 18. An earlier report of 2n = 48 for *L. subcarnosus* was probably erroneous. In spite of the morphological and chromosomal similarities of the two species, they do not hybridize in nature, even in habitats which permit their side-by-side occurrence.

The Plant Research Institute,
University of Texas, Austin,
and
The Clayton Foundation for Research.

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STUDIES ON THE CROSSABILITY OF LUPINUS TEXENSIS AND LUPINUS SUBCARNOSUS

LAWRENCE ERBE

During the period from March 17 to April 7, 1956, attempts were made to hybridize *Lupinus subcarnosus* with *L. texensis*. The work was begun just after *L. subcarnosus* began flowering. This was about two weeks later than *L. texensis* under the experimental conditions. The plants were most vigorous at this time as they had recovered from the shock of transplanting but had not yet started to decline in vigor. However, this vigorous condition could not be maintained. This factor doubtlessly was in part responsible for the low percentage of pods set from the various crosses and selfs. This is particularly true of the intraspecific crosses and selfings attempted on *L. texensis,* since these plants were the last to be worked upon and by that time they were no longer in optimum health.

The same emasculation and pollination techniques were employed as had previously proved successful on hybridization studies on the genus *Lotus* (Erbe, Master's Thesis, University of Vermont, 1955).

Stock plants of *L. subcarnosus* were obtained from a population occurring on sandy soil about ten miles west of Bastrop, Texas. Plants of *L. texensis* were obtained from a population occurring on the University of Texas campus in black clay.

On the basis of the present study, the tentative conclusion was that the two species are effectively isolated genetically. Certainly, they do not hybridize readily when subjected to experimental emasculation and pollination techniques. These experimental results as shown in Table 1 agree with the observation, presented by Turner (Madroño 14, p. 16), that there is no evidence of hybridization occurring when the two species grow sympatrically.

TABLE 1. RESULTS OF ATTEMPTED CROSSES IN LUPINUS

	No. of florets	No. of pods	Per cent of pods
Interspecific crosses:			
L. texensis × *L. subcarnosus*	52	0	0
L. subcarnosus × *L. texensis*	25	0	0
Intraspecific crosses:			
L. subcarnosus × *L. subcarnosus*	11	3	14
L. texensis × *L. texensis*	10	0	0
Selfed:			
L. subcarnosus	45	18	40
L. texensis	44	6	14

During the course of the study the writer bagged several inflorescences that were not used in the hybridization studies. Not a single floret of any of these inflorescences produced a pod. In addition, only one pod developed on the unbagged inflorescences of approximately fifteen other plants of *L. texensis*. Bee activity was almost non-existent; only one bee was

observed "working" an inflorescence. That particular inflorescence subsequently produced the only pod that developed on a *L. texensis* plant without experimental manipulation. It appears evident that pods are not produced by florets of *L. texensis* unless they have been "worked" by bees or man. Several of the unbagged inflorescences of *L. subcarnosus* set a few pods.

The Plant Research Institute,
University of Texas, Austin,
and
The Clayton Foundation for Research.

NEW NORTH AMERICAN ANDROPOGONS OF SUBGENUS AMPHILOPHIS AND A KEY TO THOSE SPECIES OCCURRING IN THE UNITED STATES[1]

FRANK W. GOULD

The Old and New World andropogons of the subgenus *Amphilophis* comprise a relatively distinct group, recognized as a separate genus by many systematists including O. Stapf, C. E. Hubbard, A. Camus, J. T. Henrard, and S. T. Blake. Both *Amphilophis* Nash and *Bothriochloa* Kuntze have been proposed as generic names for the species comprising this subgenus, with *Bothriochloa* (1891) antedating *Amphilophis* (1901). The name *Amphilophis* was first used by Trinius as a section name under *Andropogon*. Included in the section were a number of species belonging to *Vetiveria, Sorghastrum,* and *Sorghum,* as well as *Andropogon saccharoides* and its allies. Hackel, in his monograph (1889), took up *Amphilophis* as a subgenus name for the *A. saccharoides* group. *Bothriochloa* never has been officially published as a subgeneric name.

The *Amphilophis* andropogons are distinguished primarily on the basis of inflorescence characters. The pedicels, and at least the terminal rachis joints, have thickened margins and a medial groove or a broad thin membranous central area. The inflorescence characteristically is a leafless terminal panicle, with several to numerous racemose branches. In a few species there are as few as two or three branches per inflorescence.

The following new species and new name combinations are proposed in *Andropogon* rather than in *Bothriochloa* primarily to conform with the standard United States treatments of the genus (Hitchcock, 1951; Swallen, 1951; Gould, 1951; Gleason, 1952; Harrington, 1954). The Latin diagnoses have been kindly supplied by Dr. Lloyd Shinners of Southern Methodist University. Mr. Jason R. Swallen of the United States National Museum has aided in clarifying the relationships of generic and subgeneric names. The writer is indebted to the curators of the herbaria of

[1] Technical Bulletin No. TA 2384, Texas Agricultural Experiment Station, College Station, Texas.

the following institutions for the loan of specimens during the course of study: University of Arizona (ARIZ), University of California (UC), University of Michigan (MICH), University of Texas (TEX), Southern Methodist University (SMU), and Smithsonian Institution (US). Specimens of the Tracy Herbarium, A. and M. College of Texas, are cited as (TRACY). Collections of the writer are indicated by number alone. Nursery grown plants were made available through the facilities and seed introduction program of the Texas Agricultural Experiment Station, and the Plant Introduction Section of the United States Agricultural Research Service.

Andropogon springfieldii sp. nov. Perennis cæspitosa 30–80 cm. alta; nodi dense barbati pilis patentibus 3–7 mm. longis; foliorum laminæ 2–3 (–5) mm. latæ glabræ vel hispidæ prope ligulam bicrinatæ; inflorescentia dense villosa pilis 5–10 mm. longis, ramosa ramis 2–8 in axi 1–4 cm. longo, inferioribus raro ramulosis; racheos segmenta et pedicelli subæquales sulcati marginibus crassulis villosis; spicula sessilis 6.0–7.3 mm. longa, gluma inferiore acuta vel bifidula infra mediam pilosa interdum supra mediam glanduloso-punctulata, lemmatis arista 20–26 mm. longa; spicula pedicellata sterilis angusta 5 mm. longa, pedicello 1–2 mm. longior; meiosis pollinis regularis; chromosomata somatica 120.

Tufted perennial with culms 30–80 cm. tall; culm nodes densely bearded with spreading hairs, these usually 3–7 mm. long; leaf blades 2–3, occasionally to 5 mm. broad, glabrous or sparsely pustulate-hispid on the axial surface and with tufts of hair on each side of the ligule; panicle densely white-villous, with 2–8 racemose branches, these infrequently rebranched; rachis joints and pedicels about equal, with thickened, densely villous margins and a broad thin membranous central area; hairs of the inflorescence 5–10 mm. long; sessile spikelets mostly 5.5–7.3 (–8.5) mm. long, the first glume acute or minutely bifid at the apex, hairy on the lower third or half of the dorsal surface, occasionally with a faint glandular pit or depression above the middle; awn of the lemma 20–26 mm. long; pedicelled spikelet sterile, narrow, averaging 4–5 mm. long and 1–2 mm. longer than the pedicel; pollen meiosis regular; chromosome number $2n=120$.

Type: From plant grown in nursery of Texas Agricultural Experiment Station, College Station, Texas, *F. W. Gould 6642* (type, TRACY; isotypes, US, UC, TEX, SMU, ARIZ). Original seed from near Scholle, Socorro County, New Mexico (*Wayne Springfield,* 20 August 1950).

Distribution: Western Texas, New Mexico, and northern Arizona; Argentina.

Specimens examined: United States. Texas. Andrews County: Shafter Lake, *Tharp et al. 43024* (TEX). Brewster County: Alpine, *Bailey 29931* (TRACY); Chisos Mts., *Lundell 13286* (UC); Glass Mts., *Warnock W370* (TRACY) Culberson County; southeast of Van Horn, *Davis et al. 90* (TRACY); Guadalupe Mts., *Lee 67* (TEX); base of El Capitan, *Tharp* and *Gimbrede 51-1543* (TRACY); Pine Spring, *Young* in 1916 (TEX). Dawson County: *Texas Soil Survey* in 1922

(TRACY). Jeff Davis County: 30 miles west of Fort Davis, *Reeves* and *Morrow G-165* (P.I. 216668) (TRACY); northern part of county, *Burnett 9* (TEX). Presidio County: *Taylor* in 1941 (TEX). New Mexico. Chaves County: Roswell, *Hinckley* in 1936 (MICH). Lincoln County: Carrizozo, *Grassl 239* (MICH). Sierra County: Cuchillo, *Archer 416* (MICH). Socorro County: Scholle, seed collected by *Springfield* in 1950. Type collection from plants grown at College Station, Texas, *Gould 6642* (TRACY, US, UC, TEX, SMU, ARIZ). Valencia County: Paguate, *Weatherwax 2763* (TRACY). Without locality, *Wright 2103* (TRACY). Arizona. Coconino County: Havasupai Canyon, *Clover 7121* (MICH). Argentina. Buenos Aires: west of Argerich, *Eyerdam et al. 23510* (UC).

This plant most commonly has been identified as *Andropogon barbinodis* Lag., from which it differs typically in the smaller habit, narrower blades, longer nodal hairs, panicles with fewer branches, shorter axis, and more densely white-villous pedicels and rachis joints, and the lower chromosome number.

The genetical relationship of this species with other taxa of the *Amphilophis* section is obscure. The short panicle axis, few panicle branches, large spikelets, and occasional pitted glume of the sessile spikelet suggest relationship with *Andropogon edwardsianus* Gould. The latter has deeply pitted glumes and the minimum chromosome number of the New World taxa, 2n=60.

The dense villous pubescence of pedicels and rachis joints of *A. springfieldii* is not equalled in any other North American species of the *Amphilophis* section. It is, however, very similar to the condition characteristic of South American plants referable to *A. saccharoides* var. *erianthoides* Hack. The latter, undoubtedly specifically distinct from *A. saccharoides*, also has a chromosome number of 2n=60. Both *A. saccharoides* var. *erianthoides* and *A. edwardsianus* are known to occur in Uruguay. *Andropogon springfieldii* is known to the writer from Argentina and undoubtedly also is present in Uruguay.

Andropogon reevesii sp. nov. Perennis cæspitosa 30–80 cm. alta geniculata demum ramosa; nodi glabri vel puberuli; folia glauca scabra firma; vagina glabra; ligula membranacea 2–4 mm. longa; lamina 2–4 mm. lata longe acuminata glabra vel supra parce pilosa; inflorescentia 6–8 cm. longa subflabellata sat pilosa ramis 6–9 subæqualibus 3–6 cm. longis simplicibus vel inferioribus ramulosis in axi 1.0–3.5 cm. longo; racheos segmenta et pedicelli ½–¾ spiculas sessiles æquantes cum sulca media membranacea marginis crassulos ciliatos æquante; spicula sessilis 4–5 mm. longa glauca late acuta, gluma inferiore plerumque infra mediam parce pilosa superne marginibus scabris vel puberulis non pertusa; lemmatis fertilis arista 12–15 mm. longa; spicula pedicellata sterilis angusta 3.0–4.5 mm. longa pedicello longior; meiosis pollinis regularis; chromosomata somatica 120.

Perennial bunchgrass; culms mostly 30–80 cm. tall, geniculate and freely branching below in age; culm nodes puberulent to glabrous; leaves glaucous, scabrous, very firm in texture; sheaths glabrous; ligule membranous, 2–4 mm. long; blades mostly 2–4 mm. broad, relatively narrow and stiff, tapering to a long-acuminate tip, glabrous or with a few scattered

hairs on the axial surface; panicles 6–8 mm. long, somewhat flabellate, moderately hairy, with an axis 1.0–3.5 cm. long and usually 6–9 branches, these unbranched or the lowermost simply rebranched; panicle branches mostly 3–6 cm. long, the uppermost about as long as the lower; rachis joints and pedicels ½ to ¾ as long as the sessile spikelets, with a membranous medial groove about as wide as the thickened ciliate margins; sessile spikelets mostly 4–5 mm. long, glaucous, broadly acute at the apex, the first glume usually with a few coarse hairs below the middle and scabrous or minutely puberulent on the margins near the apex, pitless; awn of fertile lemma mostly 12–15 mm. long; pedicellate spikelets sterile, narrow, mostly 3.0–4.5 mm. long, longer than the supporting pedicels; pollen meiosis regular; chromosome number 2n=120.

Type: Collected 2 August 1954 from plant grown in nursery of the Texas Agricultural Experiment Station, College Station, Texas, *F. W. Gould 6647* (type, TRACY; isotypes, US, UC, MICH, TEX). Original seed from Arteago, about 15 miles east of Saltillo, Coahuila, Mexico (*R. G. Reeves* and *Judd Morrow G-640,* altitude 6,000 feet, October 15, 1953, P.I. 216183).

Distribution: Known only from the Arteago collection.

This plant is similar to *Andropogon wrightii* Hack. in general aspect but also appears close to *A. saccharoides* Swartz. From the former it differs in the stiff blades, the smaller, more reduced pedicelled spikelets, the smaller, consistently non-pitted sessile spikelets, and in the uniformly regular pollen meiosis. From the latter it differs in the narrow stiff blades, and the inflorescence with a relatively short axis, few branches, and long terminal branches. *Andropogon reevesii* has a chromosome number of 2n=120, while typical *A. saccharoides* has 2n=60 chromosomes. *Andropogon saccharoides* var. *longipaniculata* Gould has 2n=120 chromosomes but has a much larger and longer panicle, broader blades, and is a larger plant in general.

Andropogon hybridus sp. nov. Perennis cæspitosa erecta 30–80 cm. alta; nodi glabri vel puberuli; foliorum vaginæ virides glaucæ glabræ; laminæ 2–4 (–5) mm. latæ plerumque basin versus parce cilitæ sæpe in ambitu parce pilosæ; panicula 6–11 cm. longa non dense pilosa ramis 3–8 simplicibus vel inferioribus ramulosis in axi 0.6–3.5 (–4.5) cm. longo; racheos segmenta et pedicelli subæquales sulcati marginibus crassulis pilosis pilis apicem versus 5–7 mm. longis basin versus multo brevioribus; spicula sessilis 4.5–6.5 longa aristis 18–25 mm. longis, gluma inferior nitida luteo-viridi apicem versus quinquenervosa supra mediam glanduloso-pertusa, infra mediam plerumque parce pilosa; spicula pedicellata diminuta sterilis 2.2–3.6 mm. longa pedicello brevior; meiosis pollinis regularis; chromosomata somatica 120.

Perennial, with strictly erect culms in small to medium sized clumps; culms 30–80 cm. tall, moderately branched and leafy above the base; culm nodes glabrous or minutely puberulent; leaf sheaths green or glaucous,

glabrous; blades mostly 2–4 rarely –5 mm. broad, usually sparsely ciliate with long hairs near the base, often with a few hairs on the surfaces; panicles hairy but not densely so, 6–11 cm. long, usually with 3–8 primary branches on an axis 0.6 3.5, occasionally –4.5 cm. long, the lower branches often simply rebranched; rachis joints and pedicels about equal, with a broad, membranous, often dark-colored, central groove and thickened hairy margins, the hairs mostly 5–7 mm. long near the apex and much shorter towards the base; sessils spikelet 4.5–6.5 mm. long, with an awn 18–25 mm. long; first glume of sessile spikelet shiny, yellowish-green, with usually five greenish nerves apparent on the upper half, with a moderately deep glandular pit above the middle, and usually with a few stiff hairs on the lower one-third or one-half of the back; pedicelled spikelets highly reduced, sterile, mostly 2.2–3.6 mm. long and shorter than the supporting pedicel; pollen meiosis regular; chromosome number 2n=120.

Type: Texas, La Salle County, two miles east of Cotulla, *F. W. Gould 6978*, 10 November 1955 (type, TRACY; isotypes, US, UC, TEX, MICH, SMU, ARIZ). The dominant grass along a low flat graded roadside ditch in a mesquite area, growing with *Pappophorum bicolor* and weedy forbs in gravelly red-brown clay. Type and isotypes from one plant.

Distribution: South-central Texas to northeastern Mexico.

Specimens examined: Texas. Atascosa County: Jourdanton, *6223* (TRACY); Pleasanton, *6283* (TRACY). Bee County: 6.6 miles west of Beeville, *6051* (TRACY). Bexar County: San Antonio, *Higdon* in 1936 (TEX). Burnet County: Marble Falls, *5959* (TRACY). Cameron County: near San Benito, *Faulkner 94* (TRACY). Dimmit County: Asherton, *6004* (TRACY). Gillespie County: 8 miles east of Fredericksburg, *5354* (TRACY); 11 miles east of Fredericksburg, *6487* (TRACY). Gonzales County: 8.5 miles south of Smiley, *6066* (TRACY); 8.5 miles south of Smiley, *6067* (TRACY). Guadalupe County: 19 miles west of Sequin, *6939* (TRACY). Kerr County: Kerrville, *6484* (TRACY). Kleberg County: 11 miles west of Kingsville, *6043* (TRACY); Kingsville, *6034* (TRACY). La Salle County: Cotulla, *6978* (TRACY). Live Oak County: George West, *6047* (TRACY); *Cummins 12* (TRACY). Matagorda County: Palacios, *Richmon 26* (TRACY). Maverick County: 10.5 miles south Quemando, *5997* (TRACY); Eagle Pass, *6473* (TRACY); west of La Pryor, near county line, *6475* (TRACY). Nueces County: western Nueces County, *Tharp 47428* (TRACY). Real County: Camp Wood, *6952* (TRACY); Leaky, *6482* (TRACY). Travis County: 20 miles northwest of Oak Hill, *5961* (TRACY). Uvalde County: Uvalde, *6479* (TRACY); Uvalde *6226b* (TRACY). Val Verde County: 30 miles west of Del Rio, *Rose 71* (TRACY). Webb County: *Tharp 5255* (TEX). Mexico. Coahuila. Sabinas, *6471*.

This plant is intermediate between *Andropogon edwardsianus* Gould and *A. barbinodis* Lag. both in morphological characteristics and in chromosome number. From *A. edwardsianus* it differs in having broader blades, better developed upper culm leaves, more branched culms whose nodes often are puberulent, glume of sessile spikelet hairy below, panicle usually larger and more branched, and a 2n chromosome number of 120 rather than 60. From *A. barbinodis* it differs typically in the shorter, more erect, less branched culms, glabrous or puberulent nodes, narrower leaf blades, smaller panicles with fewer branches, these often all unbranched, shorter pedicellate spikelets, less hairy glume of sessile spikelets, and fewer chromosomes. In relatively few areas do plants of *A. barbinodis* have all sessile

spikelets pitted while in *A. hybridus* the sessile spikelets consistently are pitted.

Andropogon hybridus characteristically is a plant of moderately disturbed habitats. It is most frequent along low roadsides and fence-rows, often forming dense stands. Throughout its range it is consistently associated with *A. barbinodis* and either *A. saccharoides* var. *torreyanus* or *A. saccharoides* var. *longipaniculata.*

Inflorescences of plants assumed to be hybrids between *A. hybridus* (2n=120) and *A. saccharoides* var. *longipaniculata* (2n=120) have been collected at two Texas localities (Bee County, 6.6 miles west of Beeville, *6050a*; Uvalde County, 1.5 miles north of Uvalde, *6226c*). No indications of hybridization between *A. hybridus* and *A. saccharoides* var. *torreyanus* or *A. barbinodis* have been observed. It is very possible, however, that the first two taxa, with n=60 and n=30 chromosomes respectively, have produced fertile allopolyploids referable to *A. barbinodis* (n=90).

Andropogon hybridus appears to have arisen from one or more hybrids between *A. edwardsianus* (n=30) and *A. saccharoides* var. *torreyanus.* Hybridization, followed by doubling of chromosome number, could well have produced this fully fertile species. *Andropogon hybridus* seems almost certainly to be a relatively "young" species whose success is correlated with man's occupation and development of the region in which it occurs. Despite its present abundance along roads and railroad rights-of-way, the favorite collecting sites of taxonomists, this grass is poorly represented in herbaria. All but one of the collections studied and cited in this paper were made in the last 20 years. A complete search has not been made of the large herbaria for early collections, but these are certain to be few.

Andropogon palmeri (Hack.) comb. nov. *Andropogon saccharoides* Swartz subsp. *leucopogon* var. *palmeri* Hack., in DC. Monogr. Phan. 6:496. 1889. *Amphilophis palmeri* Nash, Fl. N. Amer. 17: 126. 1912.

Type: Palmer 305 "Mexico ad Rio Blanco." 1886.

Specimens examined: Specimens from plants grown at College Station, Texas, from the following seed collections. MEXICO. DURANGO: between Torreon and Durango City, *Morrow* and *Merrill G705* (P.I. 216186), between Zacatecas and Durango City, *Morrow* and *Merrill G736* (P.I. 216196). Identification of this material was made by Jason R. Swallen of the United States National Museum.

Andropogon palmeri is similar to *A. barbinodis* in growth habit and inflorescence characteristics. It differs from this species primarily in having densely villous blades and sheaths. The first glume of the sessile spikelet may or may not be glandular-pitted. Although no accurate chromosome count has been obtained, it is most likely that this species has 2n=180 chromosomes, the same as *A. barbinodis.*

ANDROPOGON BARBINODIS Lag. var. **perforatus** (Trin.) comb. nov. *Andropogon perforatus* Trin. ex Fourn. Mex. Pl. 2: 59. 1886. *A. saccharoides* subsp. *leucopogon* var. *perforatus* Hack., in DC. Monogr. Phan. 6:496. 1889. *Amphilophis perforatus* Nash, in Small, Fl. Southeast U. S.

66. 1903. *Bothriochloa perforata* Herter, Rev. Sudamer. Bot. 6:135. 1940.

Type: *Berlandier 641* "Envir. de Mexique."

Distribution: South-central U. S. and Mexico, Argentina, and Uruguay.

Specimens examined: UNITED STATES. TEXAS. Aransas County: Rockport, *Cates* in 1946 (TRACY). Bee County: west of Beeville, *6049* (TRACY). Bell County: near Little River, *Wolff 2260* (TRACY). Hidalgo County: 12 miles north of Edinburg, *6024* (TRACY). Blanco County: west of Johnson City, *5963* (TRACY). Bosque County: 12 miles northeast of Walnut Springs, *Shinners 10420* (SMU). Brooks County: 19 miles north of San Manuel, *6029* (TRACY). Brown County: Brownwood, *5681* (TRACY). Brewster County: Chisos Mts., *Sperry 396* (TRACY). Caldwell County: Luling, *6938* (TRACY). Dimmit County: north of Carrizo Springs, *McCully 32* (TRACY). Edwards County: Texas Agr. Exp. Station, Substation 14, *Cory 52473* (SMU, UC), *Sperry* in 1947 (TRACY). Gillespie County: Fredericksburg, *5965* (TRACY); east of Seguin, *6069, 6070* (TRACY). Guadalupe County: 19 miles west of Seguin, *6942* (TRACY). Hays County: Kyle, *Tharp* in 1920 (MICH). Llano County: Llano, *Wolff 3047* (TRACY); south of Valley Spring, *Smathers 14* (TRACY); Enchanted Rock, *Tharp 7699* (TEX). Maverick County: 16 miles east of Eagle Pass, *6973a* (TRACY). McCulloch County: Lohn, *Whitaker 50-16* (TRACY). McLennon County: east Waco, *Smith 306* (TEX). Mitchell County: northeast of Colorado City, *Pohl 4987* (SMU). Motley County: west of Matador, *Duvall 52-102* (*RF 556*) (TRACY). Pecos County: Fort Stockton, *Cory* in 1924 (TRACY). Palo Pinto County: west of Mineral Springs, *Whitehouse 19296* (MICH, SMU). Somervell County: north of Glen Rose, *Evans* in 1951 (TRACY). Tarrant County: *Ruth 1065* (MICH). Uvalde County: Montell, *6951* (TRACY); Sabinal, *6945* (TRACY). Young County: Graham, *Reverchon 3439* (SMU). ARIZONA. Cochise County: Douglas, *Gould* and *Haskell 4548*, in part (SMU). Pima County: Santa Rita Range Reserve, *Culley 58* (ARIZ). MEXICO. CHIHUAHUA. Agua Caliente, *LeSueur mex 051*, in part (SMU, UC); between Camargo and Parral, *Reeves* and *Morrow G–493* (P.I. 216165), in part (TRACY); north of Chihuahua City, *Reeves* and *Morrow G–362* (P.I. 216157) (TRACY). COAHUILA. 40 km. west of El Oro, *Harvey 1275*, in part (MICH); 10 miles north of Mondora, *Reeves* and *Morrow G-328* (P.I. 216121) (TRACY). DURANGO. North of Durango City, *Reeves* and *Morrow G-524* (P.I. 216122) (TRACY); between Durango City and Torreon, *Morrow* and *Merrill G-841* (P.I. 216096) (TRACY); between Durango City and Mazatlan, *Morrow* and *Merrill G-789* (P.I. 216088) (TRACY); between Durango City and Parral, *Morrow* and *Merrill G-760* (P.I. 216080) (TRACY); Ignacio Allende, *Gentry 6917* (ARIZ). HIDALGO. Ixtaccihuatl, *Purpus* in 1905 (UC); Pachuca, *Purpus 1631* (UC, MICH); north of Zimapan, *7023* (TRACY). MEXICO (or D. F.). "Envir. de Mexique," *Berlandier 641*, fragment from type (US). SAN LUIS POTOSI. Charcos, *Whiting 525* (TEX, ARIZ, MICH). VERA CRUZ: "Region d' Orizaba," *Bourgeau 2374* (US). ZACATECAS. Zacatecas, *Pringle 1761* (UC, ARIZ).

The writer's concept of this taxon is based on examination of a panicle fragment from the type and the original description by Fournier. The fragment, consisting of three inflorescence branches, was obtained for the United States National Herbarium by Dr. A. S. Hitchcock in 1907. The type is in the Trinius Herbarium at Leningrad and unavailable for study.

The following is a critical description of the fragment in the United States National Herbarium: longest raceme 6 cm.; rachis and pedicels ciliate with relatively long hairs; first glume of sessile spikelets averaging 5.8 mm. long, relatively narrow, rather thickly beset below the middle with stiff hairs, with a single moderately sized glandular pit or depression (averaging 0.23 mm. in diameter) about 2 mm. from the tip; awn of

lemma averaging 26 mm. long; pedicelled spikelets averaging 3.8 mm. long, slightly longer than the supporting pedicels.

Fournier in the original description stated, "Culmo ramiso, . . . nodis barbatis; panicula flabellata e fasciculatis divergentibus composita, . . . ".

The hybrid origin of *Andropogon barbinodis* with its high chromosome number has been previously hypothesized (Gould, 1953). It is believed that the factors for pitted spikelets, short inflorescence axis, and brittle rachis have been introduced into this taxon from *A. edwardsianus* or directly from the Old World *A. pertusus* complex.

The glume pit occurs in *A. barbinodis* in all possible gradations, from a faintly discernible glandular spot on one or two spikelets of the panicle to a large, deep pit on all sessile spikelets. From one or more centers, the pit character has become dispersed in *A. barbinodis* populations almost throughout the range of the species. In North America the pits are most consistently present in plants of central Texas and eastern Mexico. Glume pits have been observed in specimens from New Mexico, Arizona, and even southern Utah (Washington County, near Springdale, *M. E. Jones 6071,* near St. George, *Gould 1359*).

It is the intent of the writer to assign to *A. barbinodis* var. *perforatus* all plants of the species in which the sessile spikelets predominantly are pitted. This criterion is somewhat arbitrary as there is no distinct break in the pitted-spikelet series, but it does conform with the established concept of the "perforatus" entity.

Plants referable to *A. barbinodis* var. *perforatus* generally have been confused with those of *A. hybridus* and *A. edwardsianus,* the only New World species consistently having pitted sessile spikelets. The *A. barbinodis* plants are most readily distinguished from those of these species by the taller, stouter, more freely branched and less strictly erect culms, broader blades, larger panicles, larger pedicelled spikelets, and more densely hairy glume of the sessile spikelet.

Andropogon saccharoides Swartz var. **pulvinatus** var. nov. Perennis cæspitosa 70–130 cm. alta; nodi plerumque breviter barbati; folia glabra sæpe glauca, laminis 5–10 mm. latis; panicula exserta 8–16 cm. longa ramis 8–15 in axi 7–12 cm. longo, axillis atro- vel brunneo-pulvinatis; rami inferiores 2–5 cm. longi ramulosi in anthesis patentes demum contracti sed basi curvati; racheos segmenta et pedicelli pilosi pilis apicem versus 6–9 mm. longis, sulcata sulca media lata membranacea plerumque atrata; spicula sessilis 3–4 mm. longa lato-oblonga late acuta; spicula pedicellata 3 mm. longa pedicello plerumque brevior; chromosomata somatica 60.

Perennial bunchgrass; culms 70–130 cm. tall; culm nodes mostly short-bearded; leaves glabrous, often glaucous, the blades 5–10 mm. broad; panicle well exserted, 8–16 cm. long, with an axis mostly 7–12 cm. long and 8–15 primary branches; lower panicle branches 2–5 cm. long, mostly rebranched, spreading in anthesis but contracting in fruit, the bases re-

maining bowed-out; panicle branches with blackish or brownish, usually hairy pulvini in their axils; rachis joints nearly as long as the sessile spikelets, the latter overlapping for 1/5 or less of their length; rachis joints and pedicels hairy, the hairs 6–9 mm. long near the apex, shorter below; groove of pedicel broad, membranous, usually dark-colored; sessile spikelets typically 3–4 mm. long, broadly oblong, with a broadly acute apex; pedicillate spikelets about 3 mm. long, usually slightly shorter than the supporting pedicels; chromosome number 2n=60.

Type: Mexico. Coahuila, Rancho Sierra Hermosa, 40 miles west of Monclava, *F. W. Gould 6467*, 25 June 1952 (type, TRACY; isotype UC). On rocky, brushy slopes, at 6,700 feet altitude.

Distribution and specimens examined: Known only from the type collection and from plants grown at College Station, Texas, from seed from the type collection.

This variety differs from *A. saccharoides* var. *torreyanus* in the taller culms, larger panicles, spreading or loosely contracted inflorescence branches with axillary pulvini, and more widely spaced spikelets. From *A. saccharoides* var. *longipaniculata* it is distinguished by the spreading or more loosely contracted inflorescence branches, the pulvini, the more widely spaced and blunter spikelets, and the chromosome number of 2n=60 rather than 120.

Key to the native and naturalized species of Andropogon subgenus Amphilophis in the United States

I. All or some sessile spikelets pitless*

Pedicelled spikelets about as large and broad as the sessile ones.
  Sessile spikelets more than 5 mm. long. Native species . . . 7. *A. wrightii*
  Sessile spikelets less than 5 mm. long. Introduced species.
    Panicle axis shorter than the branches; sessile spikelets never pitted . . . . 9. *A. ischaemum*
    Panicle axis longer than the branches; sessile spikelets without pits or irregularly pitted . . . . 11. *A. intermedius*
Pedicelled spikelets much narrower and usually shorter than the sessile ones.
  Sessile spikelets 4.5–7.3 mm. long, awns 20–33 mm. long (18–20 in California *A. barbinodis*); spikelets pitless or both pitted and pitless on the same panicle.
    Panicle axis less than 5 cm. long; panicle branches 2–8; rachis joints and pedicels densely white villous; culms slender, not over 1 meter tall and usually much shorter; leaf blades rarely over 4 mm. broad; pollen grains averaging 36–41 microns in diameter; chromosome number 2n=120 6. *A. springfieldii*
    Panicle axis typically 5–15 cm. or more long; panicle branches typically numerous, rachis joints and pedicels villous but not densely so; culms typically stout, often over 1 meter tall; leaf blades, at least some, often 5–8 mm. broad.
      Panicles of the larger culms 14–25 cm. long; culms very stout, stiffly erect, 1.2–2.5 meters tall, bluish glaucous below the nodes; culm nodes bearded with spreading hairs 3–6 mm. long; pollen averaging 39–40 microns in diameter; chromosome number, 2n=120 . 5. *A. altus*

*Refers to circular glandular depression on outer (first) glume.

Panicles mostly 7–13 cm. long; culms curving-erect, tending to become decumbent and much-branched below in age, mostly 0.7–1.1 meters tall, not bluish glaucous below the nodes; culm nodes bearded with appressed hairs less than 3 mm. long; pollen averaging 45–52 microns in diameter; chromosome number, 2n=180.

Sessile spikelets all or mostly pitless . 8a. *A. barbinodis* var. *barbinodis*

Sessile spikelets mostly pitted . . . 8b. *A. barbinodis* var. *perforatus*

Sessile spikelets less than 4.5 mm. long, awn of lemma less than 19 mm. long; spikelets never pitted.

Awns absent or not more than 6 mm. long . . . . 1. *A. exaristatus*

Awns present, 8–18 mm. long.

Panicles 5–9, occasionally –13 cm. long; glumes ovate, dull green and most commonly with a whitish waxy bloom; pollen averaging 34–37 microns in diameter; chromosome number, 2n=60 . . . . . . 2a. *A. saccharoides* var. *torreyanus*

Panicles of the larger culms 10–20 cm. long; glumes narrowly ovate, shiny green; pollen averaging 39–42 microns in diameter; chromosome number, 2n=120; southeastern and southern Texas to northern Mexico . . . . 2b. *A. saccharoides* var. *longipaniculata*

II. All sessile spikelets pitted

Pedicelled spikelets about as large and broad as the sessile ones.

Sessile spikelets more than 5 mm. long. Native species . . 7. *A. wrightii*

Sessile spikelets less than 5 mm. long. Introduced species.

Panicle axis shorter than the lower branches . . . . . 10. *A. pertusus*

Panicle axis longer than the lower branches . . . . 11. *A. intermedius*

Pedicelled spikelets much narrower and usually shorter than the sessile ones.

Panicle axis less than 5 cm. long; primary panicle branches mostly 2–7, rarely more than 8; culm nodes glabrous or minutely pubescent.

Upper culm nodes glabrous; primary panicle branches never rebranched; first glume of sessile spikelet 5.5–7.0 mm. long, glabrous on back, with a relatively large and deep glandular pit; leaves mostly in dense basal tuft, the culm leaves reduced; leaf blades rarely over 2 mm. broad; chromosome number 2n=60 . . . . 3. *A. edwardsianus*

Upper culm nodes glabrous or puberulent; lower 1 or 2 panicle branches frequently rebranched; first glume of sessile spikelet 4.5–5.7 mm. long, usually sparsely hispid on back near base; glume pit relatively small and shallow; culm leaves well developed; blades 2–5 mm. broad; chromosome number, 2n=120 . . . . 4. *A. hybridus*

Panicle axis typically 5–15 cm. or more long; panicle branches numerous.

Panicles of the larger culms 14–25 cm. long; culms very stout, stiffly erect, 1.2–2.5 meters tall, bluish glaucous below the nodes; culm nodes bearded with spreading hairs 3–6 mm. long; panicle axis and branches often remaining "kinked" from compression in the sheath; pollen averaging 39–40 microns in diameter; chromosome number, 2n=120 . 5. *A. altus*

Panicles mostly 7–13 cm. long; culms curving-erect, tending to become decumbent and much branched below in age, mostly 0.7–1.1 meters tall, not bluish-glaucous below the nodes; culm nodes bearded with appressed hairs less than 3 mm. long; panicle axis and branches not "kinked"; pollen averaging 45–52 microns in diameter; chromosome number, 2n=180 . . . . 8b. *A. barbinodis* var. *perforatus*

1. A. EXARISTATUS (Nash) Hitchc., Biol. Soc. Wash. Proc. 41:163. 1928. *Andropogon saccharoides* var. *submuticus* Vasey ex Hack. in DC.,

Monogr. Phan. 6:495. 1889. Not *A. submuticus* Steud., 1854. *Amphilophis exaristatus* Nash in Small, Fl. Southeast. U. S. 65. 1903. *Bothriochloa exaristata* (Nash) Henr. Blumea 4:520. 1941.

Distribution: Along the Gulf Coast of Louisiana and Texas; coastal Brazil, Argentina.

2a. A. SACCHAROIDES Swartz var. TORREYANUS (Steud.) Hack. in DC., Monogr. Phan. 6:495. 1889. *Andropogon glaucus* Torr., Ann. Lyc. N. Y. 1:153. 1824. Not *A. glaucus* Retz., 1789. *Andropogon torreyanus* Steud., Nom. Bot. ed. 2. 1:93. 1840. Based on *A. glaucus* Torr. *Andropogon jamesii* Torr. in Marcy, Expl. Red River 302. 1853.

Distribution: Alabama, Missouri and Colorado to northern Mexico.

2b. A. SACCHAROIDES var. LONGIPANICULATA Gould, Field and Lab. 23(1):17–19. 1955.

Distribution: Southern and southeastern Texas to northeastern Mexico.

3. A. EDWARDSIANUS Gould, Field and Lab. 19:183–185. 1951.

Distribution: Edwards Plateau of central Texas; Argentina and Uruguay.

4. A. HYBRIDUS Gould, sp. nov.

Distribution: Southern Texas and northeastern Mexico.

5. A. ALTUS Hitchc. Contr. U. S. Nat. Herb. 17(3):308. 1913.

Distribution: Western Texas and southern New Mexico to west-central Mexico; Bolivia and Argentina.

6. A. SPRINGFIELDII Gould, sp. nov.

Distribution: Western Texas and New Mexico to northern Arizona; Argentina.

7. A. WRIGHTII Hack. Flora 68:139. 1885. *Amphilophis wrightii* (Hack.) Nash. *Bothriochloa wrightii* (Hack.) Henr., Blumea 4:520. 1941.

Distribution: New Mexico and northern Mexico.

8a. A. BARBINODIS Lag. [Gen. et Sp. Nov. 3. 1816] var. BARBINODIS. *Amphilophis barbinodis* (Lag.) Nash in Small, Fl. Southeast. U. S. 65. 1903. *Bothriochloa barbinodis* (Lag.) Herter, Sudamer. Bot. Rev. 6:135. 1940.

Distribution: Texas, southern Colorado, Utah, and California, south to Argentina.

8b. A. BARBINODIS Lag. var. PERFORATUS (Trin.) Gould, comb. nov.

Distribution: South-central U. S., Mexico, Argentina, and Uruguay.

9. A. ISCHAEMUM L. Sp. Pl. 1047. 1753. *Amphilophis ischaemum* (L.) Nash, N. Amer. Fl. 17:124. 1912. *Bothriochloa ischaemum* (L.) Keng. Contr. Biol. Lab. Sci. Soc. China Bot. Ser. 10:201. 1936.

Distribution: Widespread in tropical and temperate regions of Asia,

Africa and Europe. Established as a pasture and wayside grass in Texas and occasional elsewhere in the United States from pasture plantings.

10. A. PERTUSUS (L.) Willd., Sp. Pl. 4:922. 1806. *Amphilophis pertusa* (L.) Stapf. in Prain, Fl. Trop. Afr. 9:175. 1917. *Bothriochloa pertusa* (L.) A. Camus, Ann. Soc. Lyon n. ser. 76:164. 1931.

Distribution: Tropical and subtropical Asia, Africa, and Australia. Occasional in southern Texas as a seeded pasture grass.

11. A. INTERMEDIUS R. Br., Prodr. Fl. Nov. Holl. 202. 1810. *Amphilophis intermedia* (R. Br.) Stapf in Prain, Fl. Trop. Afr. 9:174. 1917. *Bothriochloa intermedia* (R. Br.) A. Camus, Ann. Soc. Linn. Lyon n. ser. 76:164. 1931.

Distribution: China, India, the Indo-Malay region and Australia. Introduced as a pasture grass in Texas.

Summary

Three new species, one new variety, and two new name combinations are proposed in *Andropogon,* subgenus *Amphilophis.* A key is presented to the eight indigenous and three naturalized species of this subgenus occurring in the United States. A unique feature of the key is the prominent use of the glume pit character. Of the species included in the key, the glandular glume pit is consistently present in three, consistently absent in four, and of variable occurrence in five.

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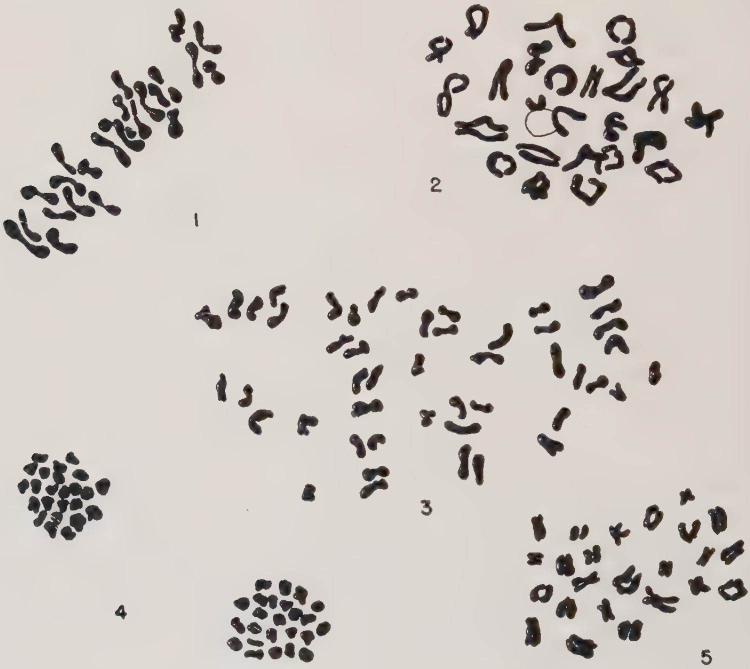
CHROMOSOME NUMBERS IN LUPINUS

LYLE L. PHILLIPS

The genus *Lupinus*, a member of the sub-family Papilionoideæ of the Leguminosæ, is a group of world-wide distribution with population centers in western United States, Europe, and South America. The present cytological study was undertaken in conjunction with a taxonomic revision of the perennial lupines of North America (Phillips, 1955) in which sixteen species and sixteen infra-specific taxa are recognized. Chromosome numbers are listed below for twenty-six of these taxa.



FIGS. 1–5. *Lupinus* meiosis and mitosis: *1, L. laxiflorus* var. *laxiflorus*, M_I, n=24; *2, L. sulphureus* subsp. *sulphureus*, Diak., n—24; *3, L. saxosus*, late Diak., n=48; *4, L. humicola*, T_I, n=24; *5, L. sericeus* subsp. *sericeus*, c-mitotic metaphase, n=24. The camera lucida drawings of the chromosomes were made at a magnification of 1940 and reduced to 970.

The chromosome number determinations were made either at diakinesis or metaphase I of microsporogenesis or metaphase of root mitosis. The meiotic material was fixed in Carnoy III (3 parts ethanol, 4 parts chloroform, and 1 part acetic acid) and smeared in aceto-carmine or propiono-carmine. Root tips were treated in oxyquinoline according to Tjio and Levan (1950) and smeared in aceto-orcein. Pollen fertility analyses were made with cotton blue lacto-phenol.

The present study on the perennial lupines and several previous reports on the chromosome numbers of Old World species (Kawakami, 1930; Savchenko, 1936; Tuschnjakowa, 1935; and Maude, 1940) make it apparent that the basic number of the genus is 12. Diploid (n=12) and tetraploid (n=24) species as well as several taxa that deviate from the basic number (n=21, 25, 26) are cited for Europe and Africa. Of the

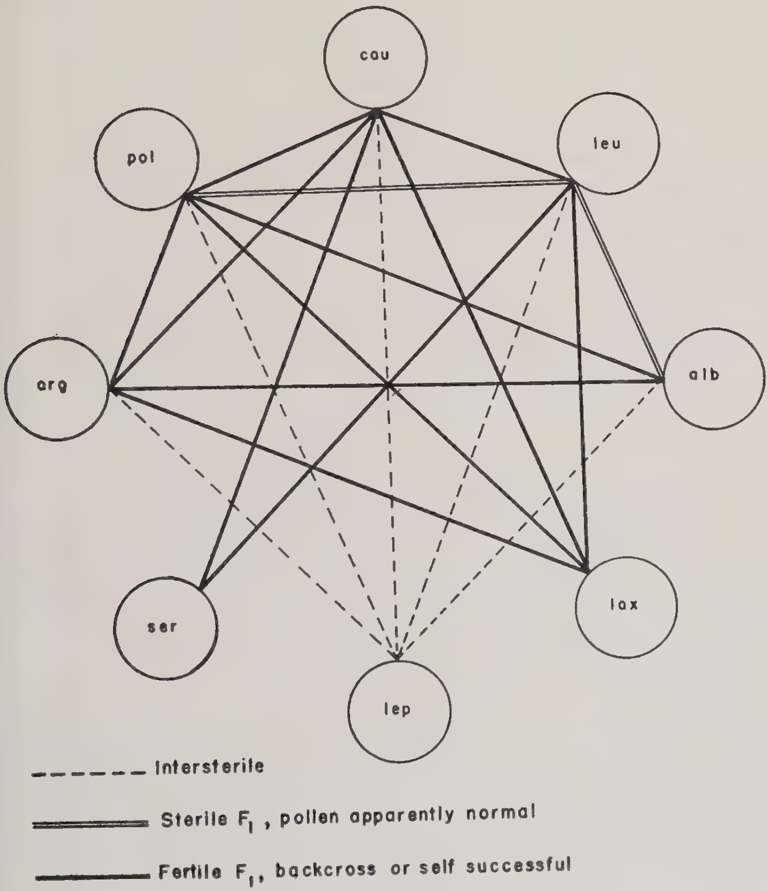


FIG. 6. Breeding behavior of eight species of *Lupinus* of the Northwestern United States. All taxa n=24: alb. = *L. albicaulis;* arg. = *L. argenteus* subsp. *argenteus;* cau. = *L. caudatus* subsp. *caudatus;* lax. = *L. laxiflorus* var. *laxiflorus;* lep. = *L. lepidus* subsp. *lepidus;* leu. = *L. leucophyllus;* pol. = *L. polyphyllus* var. *polyphyllus;* ser. = *L. sericeus* subsp. *sericeus.*

twenty-six North American taxa examined cytologically twenty are tetraploid, two are octaploid ($n=48$), and four are both tetraploid and octaploid. The octaploid chromosome level has been heretofore unreported for the genus.

In none of the four taxa which contain two chromosome "races" is this difference in chromosome number correlated with morphological dissimilarities. Apparently the genetic isolation created by chromosome doubling in these taxa has not been operative long enough to permit divergence into morphologically definitive types. In a few instances populations of octaploids are somewhat unique as compared with related tetraploids, but these unique individuals or populations fall within the variation pattern of the taxon as a whole and cannot justifiably be given specific or infraspecific recognition.

Figure 6 presents a summary of a hybridization study involving eight tetraploid species native to Northwestern United States. It can be seen that all of the interspecific crosses were successful except those crosses involving *L. lepidus*. The F_1 hybrids exhibited nearly regular meioses (occasionally lagging chromosomes were seen at metaphase I), and a fairly high degree of pollen fertility (75–85 per cent). Attempted crosses of *L. lepidus* × *L. argenteus* and *L. lepidus* × *L. leucophyllus* resulted in the production of normal seed pods containing aborted ovules. Since no such stimulatory effect on pod development was observed with other crosses involving *L. lepidus*, this is interpreted to mean that, of the species studied, *L. lepidus* is most closely related to *L. argenteus* and *L. leucophyllus*.

The apparent lack of genetic barriers between these species, demonstrable under experimental conditions, is also evident in the field where hybrid individuals often result wherever two or more species are sympatric. Occasionally hybrids and introgressants in such a sympatric association will completely blur species boundaries, but more often the discernible intermediates are relatively few in number. Presumably, the plants of hybrid nature are not able to compete with parental species except where there are uncolonized habitats available for which they are better adapted than the parents.

The low level of genetic differentiation between the species utilized in this study supplies a reasonable explanation for the extreme variability within species and for the overlapping variation pattern between many species. Species that can exchange genetic material readily are bound to be variable and difficult to separate taxonomically. Hence *Lupinus* has become known to taxonomists as a "difficult" genus.

For some of the wide-ranging taxa (*L. laxiflorus* var. *laxiflorus*, *L. sericeus* subsp. *sericeus*, *L. polyphyllus* var. *polyphyllus*) the citations listed below constitute only a portion of the collections counted. In these taxa the collections cited have been selected to reflect the geographical range from which cytological analysis has been made. The collections listed below are deposited in the Washington State College Herbarium.

Taxon	Chromosome Number (n)	Collection
L. albicaulis	24	Seattle, King County, Washington, *Phillips 690.*
	24	5 miles south of Kelso, Cowlitz County, Washington, *Phillips 667.*
	24	Mollala, Clackamas County, Oregon, *Phillips 720.*
L. argenteus subsp. *argenteus*	24	5 miles west of Bridgeport, Baker County, Oregon, *Phillips 634.*
	24	Pierce, Clearwater County, Idaho, *Phillips 786.*
	24	Alberton, Missoula County, Montana, *Phillips 860.*
	24	10 miles east of Livingston, Park County, Montana, *Phillips 855.*
	24	12 miles west of Custer, Custer County, South Dakota, *Phillips 846.*
subsp. *parviflorus*	24	5 miles east of Soda Springs, Bear Lake County, Idaho, *Phillips 792.*
L. caudatus	24	Baker, Baker County, Oregon, *Phillips 635.*
subsp. *caudatus*	24	2 miles south of Madras, Jefferson County, Oregon, *Phillips 627.*
subsp. *argophyllus*	48	Monticello, Summit County, Utah, *J. Nishitani 7–1952.*
L. humicola	24	Leavenworth, Chelan County, Washington, *Phillips 733.*
	24	Near Manhattan, Broadwater County, Montana, *Phillips 858.*
	24	Acme, Sheridan County, Wyoming, *Phillips 836*
L. laxiflorus var. *laxiflorus*	24	Omak, Okanagan County, Washington, *Phillips 606.*
	24	Winton, Chelan County, Washington, *Phillips 728.*
	24	Selah, Yakima County, Washington, *Phillips 627.*
	24	Near Mount Hood, Hood River County, Oregon, *Phillips 621.*
	24	6 miles east of Sisters, Deschutes County, Oregon, *Phillips 707.*
	24	2 miles south of White Bird, Idaho County, Idaho, *Phillips 800.*
	24	12 miles north of Boise, Ada County, Idaho, *Phillips 803.*
	48	Lyle, Klickitat County, Washington, *Phillips 683.*
	48	Underwood, Skamania County, Washington, *Phillips 610.*
var. *pseudoparviflorus*	24	Near Priest River, Bonner County, Idaho, *Phillips 852.*

Taxon	Chromosome Number (n)	Collection
	24	St. Regis, Mineral County, Montana, *Phillips 865.*
L. lepidus subsp. *lepidus*	24	Spanaway, Pierce County, Washington, *Phillips 582.*
	24	3 miles south of Goldendale, Klickitat County, Washington, *Phillips 612.*
	24	Dayville, Grant County, Oregon, *Phillips 630.*
	24	Near Ukiah, Umatilla County, Oregon, *Phillips 715.*
	24	6 miles north of Modoc Point, Klamath County, Oregon, *Phillips 892.*
subsp. *lyallii*	24	Toll Gate, Umatilla County, Oregon, *Phillips 699.*
L. leucophyllus	24	Near Thorpe, Kittitas County, Washington, *Phillips 642.*
	24	2 miles north of Spangle, Spokane County, Washington, *Phillips 876.*
	24	Goldendale, Klickitat County, Washington, *Phillips 658.*
	24	Near Pullman, Whitman County, Washington, *Phillips 842.*
	24	La Grand, Umatilla County, Oregon, *Phillips 636.*
	24	Dixie, Baker County, Oregon, *Phillips 633.*
	24	5 miles north of Boise, Ada County, Idaho, *Phillips 804.*
	48	Near Goldendale, Klickitat County, Washington, *Phillips 678.*
	48	Wapato, Yakima County, Washington, *Phillips 620.*
L. littoralis	24	Hecata Beach, Lane County, Oregon, *Kruckeberg 3315.*
L. polyphyllus var. *polyphyllus*	24	Montsanto, Thurston County, Washington, *Phillips 596.*
	24	Mission Peak, Kittitas County, Washington, *Phillips 676.*
	24	2 miles east of Livingston, Park County, Montana, *Phillips 851.*
	24	Oswego, Clackamas County, Oregon, *Phillips 646.*
	24	Near Viola, Garfield County, Washington, *Phillips 902.*
var. *prunophilus*	24	Wawawai, Whitman County, Washington, *Phillips 869.*
L. perennis subsp. *perennis*	24	4 miles east of Plymouth, Marshall County, Indiana, *Phillips 822.*

Taxon	Chromosome Number (n)	Collection
	24	Amboy, Lee County, Illinois, *Phillips 815.*
	24	Near Hanover, Lebanon County, Pennsylvania, *Phillips 830.*
subsp. *latifolius*	24	Mt. Rainier, Pierce County, Washington, *Phillips 613.*
	48	Zigzag, Clackamas County, Oregon, *Phillips 628.*
subsp. *plattensis*	24	5 miles east of Kimball, Kimball County, Nebraska, *Phillips 809.*
L. saxosus	48	10 miles south of Liberty, Kittitas County, Washington, *Phillips 689.*
L. sericeus subsp. *sericeus*	24	Maryhill, Klickitat County, Washington, *Phillips 687.*
	24	Big Timber, Sweetgrass County, Montana, *Phillips 851.*
	24	Gillette, Campbell County, Wyoming, *Phillips 849.*
	24	Orofino, Clearwater County, Idaho, *Phillips 890.*
subsp. *asotinensis*	24	Indian, Whitman County, Washington, *Phillips 792.*
	24	10 miles west of Clarkston, Asotin County, Washington, *Phillips 811.*
subsp. *sabinii*	24	Elgin, Union County, Oregon, *Phillips 736.*
L. suksdorfii	48	Glenwood, Klickitat County, Washington, *Phillips 679.*
L. sulphureus subsp. *sulphureus*	24	Kooskooskie, Walla Walla County, Washington, *Phillips 696.*
	24	2 miles east of Viola, Garfield County, Washington, *Phillips 903.*
subsp. *kincaidii*	24	Silverton, Polk County, Oregon, *Phillips 721.*
subsp. *subsaccatus*	24	10 miles south of Wenatchee, Kittitas County, Washington, *Phillips 746.*
	24	Cle Elum, Kittitas County, Washington, *Phillips 688.*
	48	Ellensberg, Kittitas County, Washington, *Phillips 674.*
	48	6 miles south of Coulee City, Grant County, Washington, *Phillips 882.*
subsp. *whithamii*	24	Butch Creek, Pend Oreille County, Washington, *Rumely & Phillips 453.*
	24	Near Nordman, Bonner County, Idaho, *Rumely & Phillips 455.*
	24	West shore of Priest Lake, Bonner County, Idaho, *Rumely & Phillips 456.*

Summary

Chromosome number determinations for 26 taxa of North America indicate twenty of these to be tetraploid (n=24), two to be octaploid (n=48), and four taxa to be both tetraploid and octaploid.

A hybridization study involving eight species of Northwest United States shows genetic incompatibility barriers to be poorly developed between these species, thus supplying a possible reason for the overlapping patterns of morphological variation found in the genus *Lupinus*.

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JEROME D. LAUDERMILK

Mr. Jerome D. Laudermilk, who passed away in January, 1956, was a general scientist. The originality of his inquisitive mind impressed those who knew him well. He read widely and probed deeply as he read. Characteristically he was not satisfied to accept Leeuwenhoek's account of his microscope until he had ground lenses and made a microscope of his own exactly according to Leeuwenhoek's formula. The structure of ancient weapons was a special field of research, and he lectured and demonstrated his models publicly and for the Pomona College Department of Military Science and Tactics. He was interested so deeply in the operations of those who deal in the occult that at one time he was kidnapped, taken to an obscure house, and convinced that his life would be longer if he did not write on the subject.

Jerry Laudermilk was a graduate of Kansas State College of Pharmacy, and he served in the United States Army in World War I. Being in ill health he spent several years in the desert near Wickenberg, Arizona, where he developed a deep interest in and knowledge of desert vegetation. He came to southern California thirty-five years ago, and he lived for the last thirty years in Claremont, where he was Research Associate in Geochemistry and Paleobotany at Pomona College. There, in association with Dr. Philip A. Munz, he investigated the food habits of extinct giant sloths by study of the dung of the animals in the caves they inhabited in the deserts near the Colorado River. This has provided knowledge of the past vegetation of the area.

His interests carried him into many problems concerned with plants, minerals, fossils, and other natural objects. In his investigation of plants Mr. Laudermilk was never satisfied with the statements in books. He went directly to nature and drew or wrote from what he found there. He was an excellent illustrator of books and scientific papers and a painter of ability. He wrote many popular articles presenting science and especially botany and geology as a layman would enjoy it, and in these he brought knowledge from many fields to bear on matters commonly approached by a single avenue. His illustrations and manuscripts found their way into such journals as Natural History, Desert Magazine, and Westways. His last work was the principal series of illustrations for the writer's textbook entitled "Plant Classification," scheduled to be published in February, 1957. Mr. Laudermilk clung to life for many months in the hope of seeing these illustrations in print, and it is a great regret to the author that he was not able to do so.—LYMAN BENSON, Department of Botany, Pomona College, Claremont, California.

ASTRAGALUS AGNICIDUS, A NEW LOCOWEED FROM HUMBOLDT COUNTY, CALIFORNIA

R. C. BARNEBY

The known history of the *Astragalus* described below goes back about twenty-five years, when Mr. Henry Tosten, the original discoverer, moved with his family to a ranch situated high in the outer North Coast Range near the divide between the South Fork of the Eel and the Mattole River in southern Humboldt County. Suffering great losses among his sheep, Mr. Tosten quickly identified this species as the culprit. In the summer of 1931 he prepared herbarium material and sent it to the late Mr. J. P. Tracy of Eureka, the outstanding authority on the flora of the region, and the specimens passed in due course to the University of California Herbarium at Berkeley, where I came across them in the winter of 1949. In May, 1954, I was able to visit the Tosten place and the genial owner obligingly took me up to the ridge above the ranch-house, the original station, where the locoweed still survived in sparing quantity. I am indebted to Mr. Tosten for the following information.

No sooner was the *Astragalus* recognized as poisonous than vigorous steps were taken to root it out. It was restricted to a wooded ridge, where the natural vegetation had been disturbed by logging, and was so abundant in early years that it was possible to collect great piles of stems for burning. Since then intermittent but never wholly successful attempts were made to control or exterminate it, and plans were afoot in 1954 to clear off the hilltop and plough it out. Mr. Tosten early assumed that the plant was an introduced weed; and it is said to be unknown to other ranchers in the community or county. A company of bark-strippers was

encamped on the site for some years before the Tosten occupancy, and this circumstance lends color to the view that it might have been brought in accidentally, possibly, as suggested by Mr. Tosten, from the Sacramento Valley. Yet it can be stated emphatically that it is not any species as yet recognized or described from the Americas. All attempts to identify the specimens with some Old World species having proved vain, I am forced to conclude that, in spite of its weedy occurrence, it is most probably native to California and requires a name.

The native status of *A. agnicidus* finds considerable support when we consider its probable relationships. It appears not to fit easily into any group described from Europe or Asia. On the typesheet Mr. Tracy remarked, in my opinion correctly, that it was near *A. umbraticus* Sheld., but differed in the pubescence and the pods. While *A. agnicidus* and *A. umbraticus* are readily distinguished at the specific level, as shown in the key below, they are much alike in general facies and organization, and together with *A. Congdoni* Wats. and *A. Paysonii* (Rydb.) Barneby form a small but homogeneous and presumably natural group in the genus. Leading technical characters common to the four species are: free stipules; thin-textured, often visibly penninerved leaflets; nodding or declined flowers and fruits; white petals; and pods shortly stipitate or subsessile, continuous with the receptacle (and hence falling naturally with the disjointing pedicels), in form obliquely linear- or lance-oblong, more or less incurved, compressed-triquetrous, grooved dorsally and fully bilocular. The three species known hitherto are all rare or highly localized. *Astragalus Congdoni* is endemic to the cismontane foothills of the Sierra Nevada, where it ranges in disjunct and scattered stations from the Mokelumne south to the Tule River, and is seemingly confined to areas of old metamorphic, sometimes partly serpentinized, bedrock. *Astragalus umbraticus* is known from only seven or eight stations, four of which lie in the Klamath Highland in southwest Oregon, on the Coquille, Rogue and Illinois rivers; from there it extends south to the lower Trinity River and Redwood Creek in Humboldt County, California; and it was collected long ago at an unspecified locality in the Coast Ranges of Yamhill County in northwest Oregon. The somewhat less closely related *A. Paysonii* is known as yet only from two records, one from the Snake-Green River divide in western Wyoming, the other at a point over three hundred miles distant to the northwest in the Clearwater Mountains of central Idaho. The distributional pattern of these species, considered individually and collectively, suggests that the section is a relatively old one, very likely composed of homogenic depleted species as defined by Stebbins (in *Madroño* 6:241–258, 1942). Stebbins has pointed out the alternative consequences of a change in environment on rare or relic species consisting of few biotypes: eventual extinction where the change is detrimental to their welfare, or regained vitality when conditions are altered to their advantage, or where competition is, even temporarily, reduced. It seems possible that disturbance of the highly competitive climax

woodland and the sudden weedy abundance of *A. agnicidus* are related phenomena. Further exploration of the more inaccessible parts of the North Coast Range may yet provide a definite answer.

The species discussed above may be distinguished by the following key:

1. Leaflets (except in a few early leaves) 15–35; flowers relatively large, the banner 9–16.5 mm., the keel 7–12.5 mm. long; cismontane Oregon and California.
    2. Stems and herbage nearly glabrous, the few scattered hairs strictly appressed and not over 0.6 mm. long; ovary and pod glabrous; Coast Ranges, from Yamhill County, Oregon to central Humboldt County, California. Stipe of the pod 0.8–1.9 mm. long, the body 1.4–2.4 cm. long, 2.6–3.6 mm. in diameter, 10–15-ovulate .... *A. umbraticus*
    2. Stems (at least above the base) and herbage villous or pilose, the longest hairs at least 0.9 mm. long; ovary and pod pubescent; southern Humboldt County and Sierra Nevada, California.
        3. Raceme compact and dense, the axis little-elongating, 2–4.5 cm. long in fruit; calyx-teeth linear or lance-acuminate, 3.3–5 mm. long; pod thinly villous-pilose, the stipe 0.3–0.4 mm., the body 11–15 mm. long, 3–3.4 mm. in diameter, 8–9-ovulate; Humboldt County........ *A. agnicidus*
        3. Raceme open, becoming loosely secund and mostly 5–20 cm. long in fruit; calyx-teeth subulate, 1–2.5 mm. long; pod more densely strigulose-villosulous, the stipe 1–2.5 mm., the body (1.5) 2–3.5 cm. long, 2.3–3.2 mm. in diameter, 23–29-ovulate; Sierra foothills........ *A. Congdoni*
1. Leaflets 7–15; flowers small, the banner about 7 mm., the keel about 5 mm. long; western Wyoming and central Idaho. Stipe of the pod 1–1.5 mm., the body 10–17 mm. long, 2.5–3.5 mm. in diameter, 8–10-ovulate........ *A. Paysonii*

Astragalus agnicidus sp. nov. Herbae elatae foliosae e radice verticali ramosa perenni, pilis debilibus patulis subsinuosis rectisque parce villosae, foliolis bicoloribus inferne pallidis ad nervum medianum barbatis, superne saturatius viridibus glabris, ciliatis, inflorescentia nigro-villosula; caules erecti et adscendentes fistulosi striati straminei (3) 4–9 dm. longi, ad medium ramosi vel subsimplices; stipulae membranaceae 4–15 mm. longae, imae ovato-triangulares amplexicaules inter se liberae, superiores lanceolato-acuminatae vel lineari-caudatae dimidium caulem amplectentes decurrentes deflexae; folia (3.5) 5–12 (16) cm. longa, superiora subsessilia, foliolis (6) 9–13-jugis petiolulatis ovato-vel lanceolato-oblongis obtusis vel emarginatis rarius acutiusculis mucronulatis (3) 5–22 mm. longis, majoribus penninerviis; pedunculi saepius 8–12 supra medium caulem emissi 5–13 cm. longi, folio subaequilongi; racemi dense (10) 15–40-flori, floribus mox patulo-declinatis, axi fructifero vix elongato (1) 2–4.5 cm. longo; bracteae hyalinae lanceolatae vel lineari-caudatae 2–6 mm. longae reflexae; bracteolae minutae vel 0; calycis nigro-villosuli tubus campanulatus pallide membranaceus 3.2–4.2 mm. longus, 2.4–3 mm. latus, dentes firmiores virides lineares vel lineari-acuminati 3.3–4.9 mm. longi; petala alba immaculata; vexillum per 45° recurvum, oblanceolato-subrhombicum emarginatum, 9.1–11 mm. longum; alae 8.3–9.2 mm. longae, laminis oblanceolatis obtusis vel oblique obovatis emarginatis subrectis 5.4–6.5 mm. longis, 1.5–2.6 mm. latis; carina 7–7.4 mm. longa, laminis semi-obovatis 3.9–4.2 mm. longis, 2–2.4 mm. latis, per 90–95° in apicem obtusum deltoideum incurvis; legumen

patulo-declinatum subsessile, stipite vix 0.4 mm. longo calyce persistenti occultato, de visu laterali anguste lanceolatum paullo incurvum 11–15 mm. longum, 3–3.4 mm. latum, basi obtusum, apice in rostrum anguste triangulari-acuminatum cuspidatum angustatum, triquetro-compressum, sutura ventrali prominula concave arcuata carinatum, dorso anguste sulcatum, valvulis tenuibus piloso-villosulis demum chartaceis reticulatis stramineis, late inflexis, septo completo 1.5–2.2 mm. lato; ovula 8–9; semina (vix matura) brunnea laevia 1.7–2.1 mm. longa.

Astragalo umbratico Sheld. affinis, sed caulibus elatis, pube magis copiosa patula villosa multo longiori, dentibus calycinis elongatis, necnon legumine breviori villosulo 8–9 (nec 10–15)-ovulato summopere distincta.

The species name *agnicidus* is derived from *agnus*, lamb, and *caedere*, to kill; the species was first brought to notice by its reputedly poisonous qualities.

Specimens examined. CALIFORNIA. "Local on Tosten & Peirce Ranch, near Bear Buttes, 4 miles s. of Miranda, Humboldt County, alt. about 2500 ft., June 7, 1931, *Henry Tosten* ex herb. *J. P. Tracy.* Said to be a sheep poison and attempted to be eradicated, fall of 1931" (type, UC, two sheets, *502991, 502992*). Topotypes: August 20, 1931, *J. C. Taris Jr.*, UC; May 19, 1954, just coming into flower, on brushy logged-over ridge, *Barneby 11570* (CAS, RSA, author's coll.).

Loan of the material at the Herbarium of the University of California, above cited, is hereby gratefully acknowledged.

Wappingers Falls, New York.

NOTES AND NEWS

ANEMOPSIS CALIFORNICA IN OREGON. An apparently well-established clump of *Anemopsis californica* was found in an roadside irrigation ditch, along Crystal Springs Road about one mile southwest of the bridge that crosses Lost River, Klamath Falls, Oregon, on August 15, 1955 (*Pengelly 743*). The plant was associated with cattails (*Typha*) and arrow-leaf (*Sagittaria*); however, the ditch passes through typical *Artemisia tridentata* association. This appears to be the first record of the occurrence of this species in Oregon, the nearest known locality to the south being near the mouth of the Sacramento River.—RUSSELL PENGELLY, Klamath Falls, Oregon.

Some publications of interest follow:

Responses of Vegetation to Fire, by James R. Sweeney. University of California Publications in Botany 28 (4): 143–250, pls. 12–27, 10 figs. in text. 1956. $2.00. University of California Press, Berkeley 4, California. A study of the effects of chaparral fires upon herbaceous vegetation.

The Genus Clarkia, by Harlan Lewis and Margaret Ensign Lewis. University of California Publications in Botany 20 (4): 241–392, 28 figs. in text. 1955. $2.00. University of California Press, Berkeley 4, California. A monograph of the genus based upon a many-faceted, biosystematic approach to the problem.

Variation and Genetic Relationships in the Whitlavia and Gymnobythus Phacelias, by George Willson Gillett. University of California Publications in Botany 28 (2): 19–78, pls. 3–5, 16 figs. in text. 1955. $1.00. University of California Press, Berkeley 4, California. A genetic analysis and systematic treatment of two of the seven subgenera of the genus *Phacelia*.